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**Die Gattung *Sphinginopalpus* Pic (Coleoptera: Malachiidae)
im südlichen Afrika
(36. Beitrag zur Kenntnis der Fauna Afrikas)**

von

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DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

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ABSTRACT

The species of the genus *Sphinginopalpus* Pic occurring in southern Africa are revised. From a total of 13 species placed by Champion (1922) in the genus 11 remain in *Sphinginopalpus*. The subgenus *Sphinginafricanus* is described to include all species in which the third segment of the maxillary palps is elongate in the female, namely *atripennis* Champion, *bilineaticeps* Pic, *martini* Pic, *formicarius* (Gorham) and the new species *pallidicornis*, *delicatulus*, *reavelli*, *complicatus*, *nerinaensis*, *endroedyi*, *tergalis*, *bimaculiceps*, *indengensis*, *consimilis*, *recurvus*, *recurvus* ssp. *planicornis*, *repandus*, *emarginatus*, *reductosetosus*, *tubulatus*, *natalensis*, *obtusodentatus* and *unisetosus*. The following species remain in *Sphinginopalpus* s.str.: *flavomarginatus* Champion, *tetrastigma* Champion, *albilabris* (Boheman), *oneili* Pic, *longidens* Champion, *bidens* Champion, *rudebecki* Wittmer, and the new species described: *pallidipalpis*, *triangulatus*, *orientalis*, *lesothoensis*, *orangensis*, *hanglipensis*, *rufithorax*, *nigrithorax*, *capensis*, *dentifrons*, *variceps*, *complexus*, *politipennis*, *trispinopsis*, *leucosideae*, *amatolensis*, *nelshoogtensis*, *nelshoogtensis* ssp. *transformatus*, *quadratipalpus*, *trimaculatus*, *tridensmimus*, *dwesaensis*, *nigriceps*, *uitsoekensis*, *curvispinus*, *acutispinus*, *majeri*, *expansus*, *oculimaculatus*, *zulu*, *politus*, *levemaculatus*, *trispinus*, *productus*, *wezaensis*, *bedfordensis*, *zimbabwensis*, *basutolandicus*, *breytenbachae*, *elongatidens*, *karkloofensis*, *nylsvleyensis* and *tridens*. Some species described as females had to be placed under *incertae sedis*: *Chalichorus collaris* Boheman (*Sphinginopalpus* subgen. *Sphinginafricanus*), *Sphinginopalpus barkeri* Pic (*Sphinginafricanus*), *Chalichorus myrmecodes* Boheman (*Sphinginopalpus* s. str.), *Chalichorus albifrons* Boheman (*Sphinginopalpus* s. str.).

MATERIAL UND VERDANKUNGEN

Für die Bearbeitung lag mir u. a. das ausserordentlich reichhaltige Material des Transvaal Museums, Pretoria, zur Verfügung, das fast ausschliesslich durch meinen lieben Freund Dr. Sebastian Endrödy-Younga zusammengetragen wurde. Ihm und den vielen anderen Kollegen die mir Material und Typen zum Studium zur Verfügung stellten, sei hier herzlichst gedankt.

Meinen besonderen Dank spreche ich auch Herrn Prof. Dr. R. Guggenheim und seinen Mitarbeitern R. Colombo und Evi Zuberbühler vom Labor für Rasterelektronenmikroskopie der Universität Basel aus, für die vielen Aufnahmen die ich dort machen durfte. Ebenso gilt mein Dank Herrn Karel Majer für die zahlreichen mit grosser Geduld und Sachkenntnis ausgeführten Strichzeichnungen.

Verwendete Abkürzungen:

AMG = Albany Museum, Grahamstown, Dr. F. W. Gess
 BM = British Museum (The Natural History Museum), London, Mr. D. Kempster
 MP = Muséum de Paris, Mr. J. J. Menier
 NCI = National Collection of Insects, Pretoria, Mr. R. Oberprieler
 NHMB = Naturhistorisches Museum, Basel, Dr. M. Brancucci
 NMB = National Museum, Bloemfontein, Prof. Dr. S. Louw
 RS = Rijksmuseum, Stockholm, Dr. P. Lindskog
 SAM = South African Museum, Cape Town, Mrs. M. Cochrane
 TMP = Transvaal Museum, Pretoria, Dr. S. Endrödy-Younga
 ZML = Zoological Museum, Lund, Dr. R. Danielsson

EINFÜHRUNG

Champion (1922) revidierte die Vertreter der Gattung *Sphinginopalpus* Pic aus dem südlichen Afrika. Er zählte 13 Arten auf und beschrieb die Untergattung *Chalicatorophasis* mit der Art *raffrayi*. Diese Untergattung stellt eine eigene Gattung dar und muss von *Sphinginopalpus* getrennt werden. Sie steht den mit *Colotes* verwandten Gattungen nahe und hat wie diese 4-gliedrige Vordertarsen bei den ♂, nebst weiteren Merkmalen, auf die in einer separaten Publikation eingetreten wird.

Die von Pic als *Sphinginopalpus formicoides* nach 1 ♀ beschriebene Art, gehört nicht in diese Gattung und wird provisorisch zu *Chalicatorophasis* **comb. nov.** gestellt.

Bei der Bearbeitung der Arten ergab sich, dass sie in zwei gut differenzierte Gruppen aufgeteilt werden können. Als Typus-Art von *Sphinginopalpus* hat *oneili* Pic, 1903, zu gelten. Die Arten von *Sphinginopalpus* s. str. zeichnen sich alle durch einen mehr parallelen Körper aus. Insbesondere die Flügeldecken (Abb. D, E) sind in beiden Geschlechtern weniger aufgewölbt. Bei ♂ und ♀ sind die Schulterbeulen normal ausgebildet. Als besonderes Merkmal der ♀ (Abb. F) ist das breite, beilförmige letzte Glied der Maxillarpalpen anzusehen. Die Maxillarpalpen der ♂ sind stark vergrößert und vielförmig gebildet und geben sehr brauchbare Merkmale für die Unterscheidung der Arten ab.

Für die zweite Gruppe von Arten errichte ich die Untergattung *Sphinginafricanus* **subgen. nov.** mit der Typus-Art *recurvus* **sp. nov.** Diese Untergattung hat einige Merkmale mit *Sphinginopalpus* s. str. gemeinsam, so z. B. den Bau des Kopfes, der meistens breiter ist als der Halsschild, die vergrößerten Maxillarpalpen bei den ♂, den meistens länger als breiten Halsschild, dessen vorderer Teil stark aufgewölbt, zur Basis verengt und abgeflacht ist, sowie die 5-gliedrigen Vordertarsen bei ♂ und ♀. Als besonderes Unterscheidungsmerkmal der neuen Untergattung ist die Form der Flügeldecken zu betrachten, die breit oval und stark aufgewölbt sind (Abb. A, B); Schulterbeulen bei den ♂ vorhanden, manchmal mit kurzem angedeutetem Längswulst dahinter. Bei den ♀, die meistens flügellos sind, sind die Schulterbeulen stark zurückgebildet und fehlen ganz, oder nur als kleines spitzes Gebilde vorhanden. Das Endglied der Maxillarpalpen ist schmal und lang (Abb. A, C) und nicht beilförmig wie bei *Sphinginopalpus* s. str. (Abb. F). Die Fühler sind meistens länger, oder so lang wie die Flügeldecken, bei *Sphinginopalpus* s. str. meistens um 1/4 bis 1/5 kürzer als diese. Der Halsschild ist seitlich, auf dem abgeflachten Teil, bei *Sphinginafricanus* weniger deutlich eingedrückt (Abb. G) als bei *Sphinginopalpus* s. str. (Abb. H). Bei beiden Gruppen bilden die Eindrücke eine kurze Längsrippe an ihrem Innenrande, die bei *Sphinginopalpus* s. str. deutlicher ist als bei der Untergattung.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

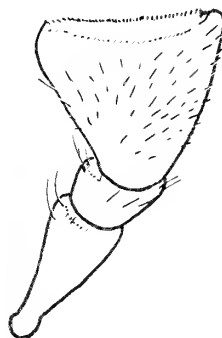
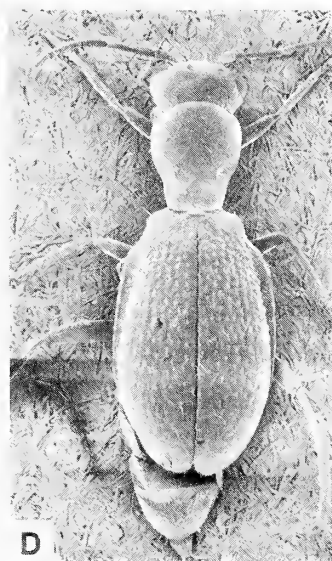
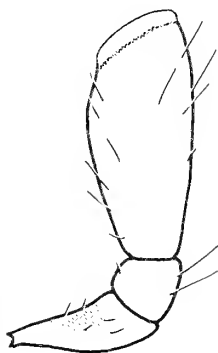
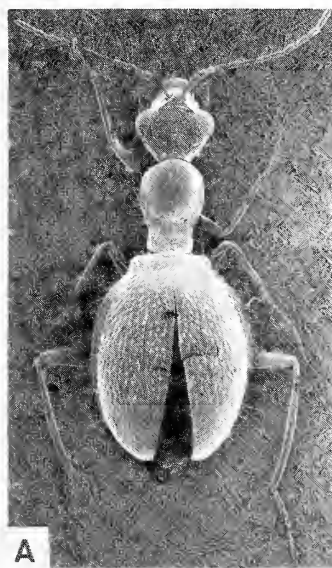


Abb. A-F. A-C. *Sphinginopalpus* (*Sphinginafricanus*) *recurvus* sp. nov. ♀: A, Gesamtansicht (x17); B, *idem* fast im Profil (x17); C, Maxillarpalpus. D-E. *Sphinginopalpus* s. str. *albilabris* (Boheman) ♀ (x25): D, Gesamtansicht; E, *idem* fast im Profil. F. *Sphinginopalpus* s. str. *orangensis* sp. nov. ♀, Maxillarpalpus.

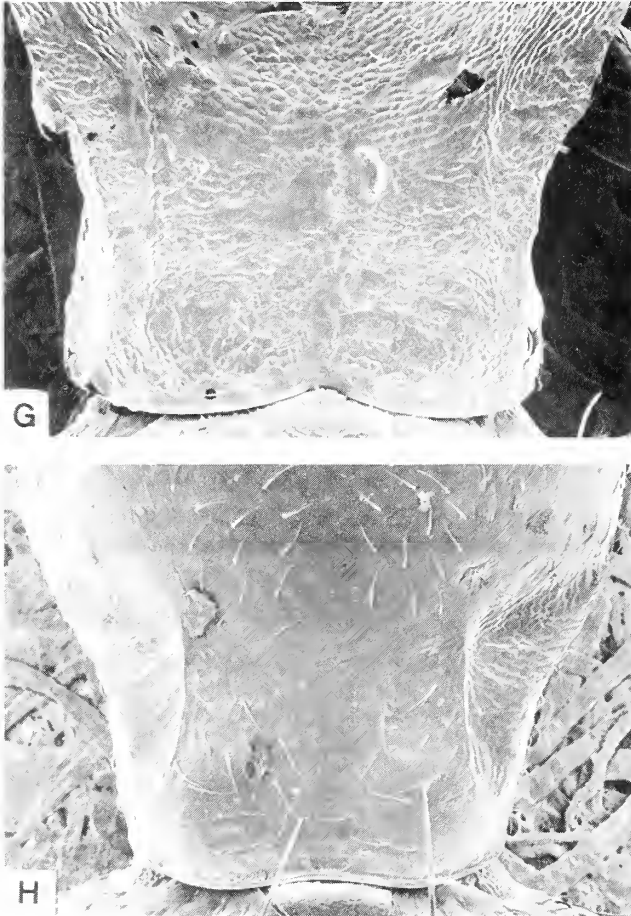


Abb. G-H. Basis des Halsschildes ♀ (x170): G, *Sphinginopalpus* (*Sphinginafricanus*) *recurvus* sp. nov.; H, *Sphinginopalpus* s. str. *albilabris* (Boheman).

Ein paar Arten die nur nach ♂ beschrieben werden, stelle ich provisorisch zu *Sphinginopalpus* s. str. bis die dazugehörigen ♀ aufgefunden werden.

Damit die letzten Abdominalsegmente etc. untersucht und gezeichnet werden konnten, wurde das Abdomen in einer Lösung von 15- 20% KOH mit Wasser während 1 bis 2 Minuten aufgekocht. Dabei war es besonders bei Sternit 8 nicht zu vermeiden, dass dieses, wenn es ganz oder teilweise im rechten Winkel zu Sternit 7 stand, flachgelegt werden musste, um ein Zeichnen zu ermöglichen. Dies ist zu berücksichtigen, wenn das Sternit 8 am Abdomen mit den Zeichnungen verglichen wird, ohne es separat auszubreiten. Das Tergit 8 ist apikal mehr oder weniger breit nach innen umgeschlagen, auf den Zeichnungen ist diese Stelle mit einer punktierten Linie oder einer dunklen Stelle eingezeichnet.

Die in den Beschreibungen vorkommenden Zahlen in Klammern (zum Beispiel: 17x15) zeigen das Verhältnis der Länge zur Breite an oder umgekehrt; sie wurden bei einer Vergrößerung von 32x gemessen.

INCERTAE SEDIS

Verschiedene Arten sind nach ♀ beschrieben worden. Es ist momentan unmöglich sie zu bestimmen, oder den Arten zuzuordnen, die nach ♂ beschrieben wurden, oder gar zu synonymisieren, wie es Champion (1922) versucht hat. Es müssten Merkmale gefunden werden, die es erlauben, die ♀ zu unterscheiden. Dies ist bisher nicht möglich gewesen und wir müssen diese Arten vorläufig unter "incertae sedis" aufführen.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

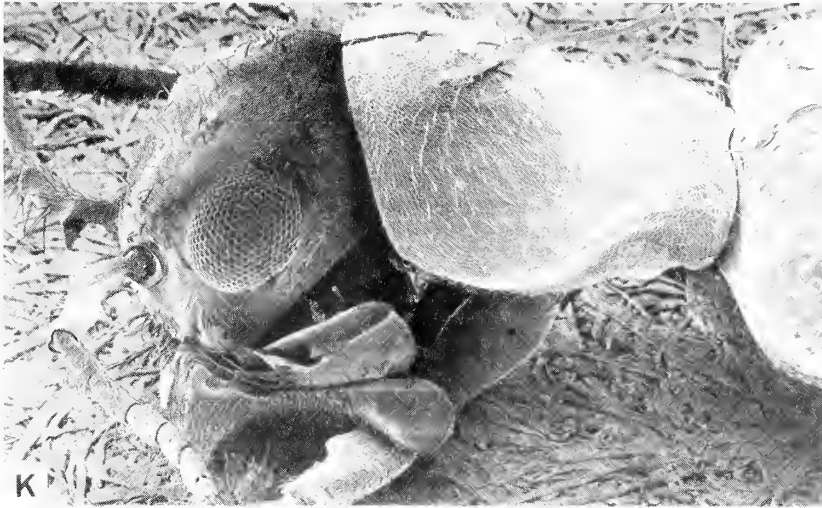
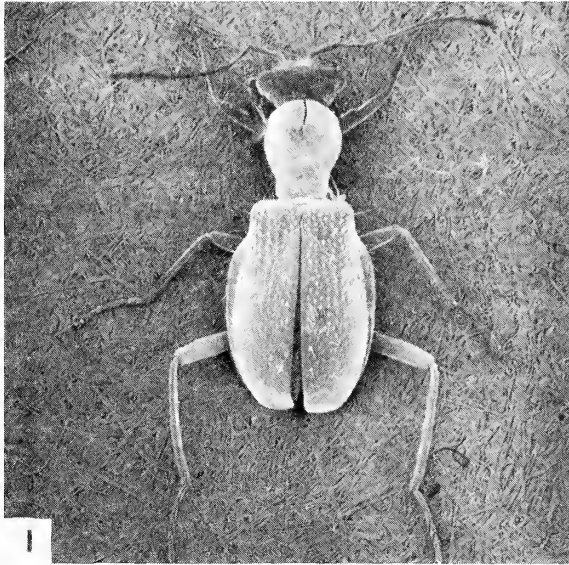


Abb. I-K. *Sphinginopalpus* (*Sphinginafricanus*) *recurvus* sp. nov. ♂: I, Gesamtansicht (x17); K, Kopf und Halsschild fast im Profil (x75).

***Sphinginopalpus (Sphinginafricanus) collaris* (Boheman)**

Chalicorus collaris Boheman, 1851: 478.

Sphinginopalpus collaris (Boheman) - Champion, 1922: 331.

Holotypus ♀ im RS.

***Sphinginopalpus (Sphinginafricanus) barkeri* Pic**

Sphinginopalpus barkeri Pic, 1904: 65. - 1911: 175. - Champion, 1922:330.

Holotypus ♀ im MP.

***Sphinginopalpus s. str. myrmecodes* (Boheman)**

Chalicorus myrmecodes Boheman, 1851: 475.

Sphinginopalpus myrmecodes (Boheman) - Champion, 1922: 330.

Holotypus ♀ im RS.

Die von Champion, 1922, als *myrmecodes* bestimmten und beschriebenen ♂ ♀ Exemplare mit Fundorten "mouth of Umkomaas River" und "Seymour" gehören zu *amatolensis* Wittmer. Die verbleibenden ♀ von anderen Fundorten sind unbestimmbar.

***Sphinginopalpus s. str. albifrons* (Boheman)**

Chalicorus albifrons Boheman, 1851: 476.

Sphinginopalpus albifrons (Boheman) - Champion, 1922: 330.

Der Holotypus dieser Art war trotz eifrigem Suchen im RS nicht aufzufinden, sodass auch sie unter "*incertae sedis*" aufgeführt wird. Der Färbung nach könnte es sich um 1 ♂ handeln, was auch Champion, 1922, vermutete.

BESTIMMUNGSTABELLE FÜR DIE ARTEN DER GATTUNG *SPHINGINOPALPUS* PIC

1. Letztes Glied der Maxillarpalpen bei den ♀ schmal (Abb.C)
 - Sphinginafricanus* subgen. nov2
- Letztes Glied der Maxillarpalpen bei den ♀ stark verbreitert, beilförmig (Abb. F)
 - Sphinginopalpus s. str.*24
2. Fühlerglied 1 bei den ♂ einfach, ohne Zahn3
- Fühlerglied 1 bei den ♂ gezahnt5
3. Spitzen von Sternit 8 nach innen gebogen4
- Spitzen von Sternit 8 nach aussen gebogen (Abb. 6)
 - 1. *S. (S.) atripennis* Champion
4. Apex von Tergit 8 mit je einer kurzen Spitze seitlich und einer langen mittleren Spitze (Abb. 12).
Flügeldecken an den Seiten hell gesäumt
 - 2. *S. (S.) pallidicornis* sp. nov.
- Apex von Tergit 8 gerundet, fast halbkreisförmig, in der Mitte schwach ausgerandet (Abb. 18).

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

- Flügeldecken einfarbig schwarz
3. *S. (S.) delicatulus* sp. nov.
5. Wenigstens 1 Fühlerglied zwischen 3 und 7 mehr oder weniger verbreitert (*)6
 – Keines der Fühlerglieder 3 bis 7 verbreitert8
6. Fühlerglieder 3 oder 4 am breitesten. Apex von Tergit 8 in der Mitte nicht in 2 kleine, kurze Fortsätze ausgezogen7
 – Fühlerglied 5 am breitesten (Abb. 24). Apex von Tergit 8 fast gerade abgestutzt, in der Mitte in 2 kleine, kurze Fortsätze ausgezogen (Abb. 25)
 4. *S. (S.) bilineaticeps* Pic
7. Fühlerglied 3 am breitesten (Abb. 30). Tergit 8 schwach, breit ausgerandet, in der Mitte kurz, schmal nach innen gefaltet (Abb. 31). Spitzen von Sternit 8 lang, nach aussen gebogen (Abb. 32)
 5. *S. (S.) reavelli* sp. nov.
 – Fühlerglieder 3 und 4 am breitesten (Abb. 103). Tergit 8 am Apex jederseits breit gerundet, Mitte schwach ausgerandet, mit *recurvus* übereinstimmend (Abb. 97). Spitzen von Sternit 8 kräftig, nach innen gebogen (Abb. 98)
 16. *S. (S.) recurvus planicornis* n.ssp.
8. Apex von Tergit 8 in der Mitte vorstehend9
 – Apex von Tergit 8 gerade bis mehr oder weniger tief ausgerandet11
9. Apex von Sternit 8 aus breiten Teilen bestehend10
 – Apex von Sternit 8 aus schmalen, langen Fortsätzen bestehend, die an der Spitze nach innen oder nach aussen verlängert sind (Abb. 38)
 6. *S. (S.) complicatus* sp. nov.
10. Tergit 8 gegen die Spitze verschmälert, diese in einen kleinen abgesetzten Fortsatz ausgezogen (Abb. 43). Sternit 8 zur Spitze verschmälert, aber nicht in eine scharfe Spitze ausgezogen (Abb. 44). Fühlerglied 1 mit einem scharfen Zahn nach der Mitte (Abb. 42), davor nicht ausgerandet. Flügeldecken einfarbig schwarz
 7. *S. (S.) nerinaensis* sp. nov.
 – Tergit 8 zur Spitze breiter, Spitze stumpf, wenig vorstehend (Abb. 50). Sternit 8 in 2 scharfe nach innen gebogene Spitzen ausgezogen (Abb. 51). Fühlerglied 1 mit einem Zahn an der Basis, davor ausgerandet (Abb. 49). Flügeldecken schmal gelblichweiss gesäumt
 8. *S. (S.) endroedyi* sp. nov.
11. Zwischen der Ausrandung von Tergit 8 befinden sich keine zusätzliche, lange, schmale Fortsätze12
 – Zwischen der Ausrandung von Tergit 8 befinden sich 2 lange, schmale Fortsätze (Abb. 57)
 9. *S. (S.) tergalis* sp. nov.
12. Spitzen von Sternit 8 nach innen gebogen13
 – Spitzen von Sternit 8 nach aussen gebogen19
- (*) Hierher gehört auch *S. (S.) reductosetosus* Wittmer, dessen Fühlerglied 5 auch, jedoch nur sehr wenig verbreitert ist (in dieser Tabelle unter 19. aufgeführt). Von *bilineaticeps* Pic durch die sehr verschiedenen Terminalia etc. zu unterscheiden, vergleiche mit Abb. 116-123.

13. Einschnitt am Apex von Tergit 8 ca. 1/3 der Länge erreichend (in der Mitte gemessen)14
– Einschnitt am Apex von Tergit 8 deutlich kürzer als 1/3 der Länge17
14. Innensack des Aedeagus mit mehreren, oder ohne stark sklerotisierte Hörnchen. Spitze von Fühlrglied 1 nach innen gerichtet15
– Innensack des Aedeagus mit nur 1 stark sklerotisierten Hörnchen (Abb. 67-68). Spitze von Fühlrglied 1 nach aussen gerichtet (Abb. 62)
10. *S. (S.) bimaculiceps* sp. nov.
15. Sternit 8 jederseits mit 2 kurzen Borsten16
– Sternit 8 jederseits mit nur 1 langen Borste (Abb. 73)
11. *S. (S.) isidengensis* sp. nov.
16. Innensack des Aedeagus mit 2 oder mehreren stark sklerotisierten Hörnchen (Abb. 82)
12. *S. (S.) martini* Pic
– Innensack des Aedeagus ohne stark sklerotisierte Hörnchen (Abb. 85)
13. *S. (S.) consimilis* sp. nov.
17. Aedeagus mit stark sklerotisierten Hörnchen18
– Aedeagus ohne stark sklerotisierte Hörnchen (Abb. 92-93)
14. *S. (S.) formicarius* (Gorham)
18. Tergit 8 am Apex wenig tief eckig eingeschnitten (Abb. 96)
15. *S. (S.) recurvus* sp. nov.
– Tergit 8 am Apex zuerst nach innen abgeschrägt, dann kurz eingeschnitten (Abb. 107)
17. *S. (S.) repandus* sp. nov.
19. Sternit 8 mit 1 oder 2 langen Borsten jederseits20
– Sternit 8 ohne Borsten (Abb. 114)
18. *S. (S.) emarginatus* sp. nov.
20. Sternit 8 mit 2 langen Borsten jederseits21
– Sternit 8 mit 1 langen Borste jederseits23
21. Die Spitzen am Apex von Sternit 8 sind lang, fast gerade, oder nur leicht nach aussen gebogen22
– Die Spitzen am Apex von Sternit 8 sind sehr kurz, hakenartig nach innen gebogen (Abb. 121)
19. *S. (S.) reductosetosus* sp. nov.
22. Ausser den beiden nur leicht nach aussen gebogenen Spitzen am Apex von Sternit 8, sind 2 scharfe nach vorne gerichtete Spitzen vorhanden (Abb. 128)
20. *S. (S.) tubulatus* sp. nov.
– Nur 2 leicht nach aussen gebogene Spitzen am Apex von Sternit 8 vorhanden, die beiden nach vorne gerichteten Spitzen fehlen (Abb. 134)
21. *S. (S.) natalensis* sp. nov.

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23. Sternit 8 lang, beide Teilstücke vollständig getrennt (Abb. 142). Tergit 8 dreieckig, ziemlich tief eingeschnitten (Abb. 141)
22. *S. (S.) obtusodentatus* sp. nov.
- Sternit 8 kürzer, die beiden Teilstücke in der Mitte durch feines Gewebe verbunden (Abb. 148)
Tergit 8 schwach, breit ausgerandet (Abb. 147)
23. *S. (S.) unisetosus* sp. nov.
24. Fühlerglied 1 bei den ♂ ohne Zahn25
– Fühlerglied 1 bei den ♂ nach der Basis ausgerandet und mit Zahn versehen27
25. Fühlerglied 1 schmal, nirgends stark verbreitert26
– Fühlerglied 1 gegen die Mitte stark verbreitert und gegen die Spitze wieder ein wenig verschmälert (Abb. 152)
24. *S. s. str. pallidipalpis* sp. nov.
26. Apex von Tergit 8 drei Spitzen bildend, die mittlere am grössten und längsten (Abb. 160)
25. *S. s. str. flavomarginatus* Champion
– Apex von Tergit 8 drei Spitzen bildend, die mittlere ist kleiner und kürzer als die seitlichen (Abb. 167)
26. *S. s. str. triangulatus* sp. nov.
27. Halsschild rotbraun oder orange, selten mit einem dunklen Flecken in der Mitte28
– Halsschildschwarz, abgesetzte Basis mehr oder weniger breit hell, selten ist der ganze Halsschild schwarz33
28. Apex von Tergit 8 etwas eingeschnitten oder ausgerandet, oder in zackiger Linie verlaufend29
– Apex von Tergit 8 gerundet, ohne Einschnitt (Abb. 178)
27. *S. s. str. orientalis* sp. nov.
29. Apex von Sternit 8 mit nach innen gekrümmten Spitzen30
– Apex von Sternit 8 mit nach aussen gebogenen Spitzen31
30. Apex von Tergit 8 gerundet eingeschnitten (Abb. 180)
28. *S. s. str. lesothoensis* sp. nov.
– Apex von Tergit 8 in zackiger Linie verlaufend (Abb. 186)
29. *S. s. str. orangensis* sp. nov.
31. Die beiden Seiten von Sternit 8 stellenweise zusammen-gewachsen32
– Die beiden Seiten von Sternit 8 vollständig voneinander getrennt (Abb. 192)
30. *S. s. str. tetrastigma* Champion
32. Kopulationsapparat in einen langen, schmalen Fortsatz ausgezogen, dessen Spitze ventralwärts gebogen ist (Abb. 195- 196)
31. *S. s. str. hanglipensis* sp. nov.
– Kopulationsapparat normal gebaut, ohne langen, schmalen Fortsatz (Abb. 207)
32. *S. s. str. rufithorax* sp. nov.

33. Flügeldecken mit einem durchgehenden weisslichen oder gelblichen Querband vor der Mitte34
 – Flügeldecken anders gezeichnet35
34. Halsschild einfarbig schwarz. Apex von Sternit 8 mit 2 grossen spitzen Zähnen (Abb. 212)
 33. *S. s. str. nigrithorax* sp. nov.
 – Halsschild schwarz mit heller Basis. Apex von Sternit 8 mit 2 kleinen hakenartigen Zähnen (Abb. 218)
 34. *S. s. str. capensis* sp. nov.
35. Apex von Sternit 8 jederseits in mehr oder weniger lange, meist schmale Fortsätze ausgezogen, oder nach innen gerichtete Spitzen bildend48
 – Apex von Sternit 8 jederseits eine mehr oder weniger grosse, breite Fläche, nicht in schmale Fortsätze ausgezogen, apikal keine Spitzen bildend36
36. Vorderstirne flach, ohne spitzen Zahn in der Mitte37
 – Vorderstirne mit einem kleinen, spitzen Zahn in der Mitte (Abb. 222)
 35. *S. s. str. dentifrons* sp. nov.
37. Apex von Tergit 8 in der Mitte mehr oder weniger tief eingeschnitten, manchmal ist der Einschnitt schwer sichtbar, z. B. bei *albilabris*38
 – Apex von Tergit 8 in der Mitte mehr oder weniger vorstehend, bis fast gerade, nicht eingeschnitten40
38. Die beiden Teile von Sternit 8 sind nicht durch loses Gewebe miteinander verbunden39
 – Die beiden Teile von Sternit 8 sind durch loses Gewebe miteinander verbunden (Abb. 231)
 36. *S. s. str. variceps* sp. nov.
39. Apex von Tergit 8 in der Mitte kaum merklich eingeschnitten (Abb. 236). Sternit 8 weniger komplex gebaut (Abb. 237)
 37. *S. s. str. albilabris* (Boheman)
 – Apex von Tergit 8 in der Mitte zuerst breit und dann ziemlich tief eingeschnitten (Abb. 243). Sternit 8 sehr komplex gebaut (Abb. 244)
 38. *S. s. str. complexus* sp. nov.
40. Apikalrand von Tergit 8 in der Mitte eckig vorstehend41
 – Apikalrand von Tergit 8 in der Mitte, wenn vorstehend, dann nur wenig, nicht eckig, sondern gerundet oder fast gerade43
41. Apikalrand von Tergit 8 in der Mitte in spitzem Winkel vorstehend, nicht eingeschnitten42
 – Apikalrand von Tergit 8 in der Mitte vorstehend und kurz eingeschnitten (Abb. 249)
 39. *S. s. str. politipennis* sp. nov.
42. Fühlerglied 1 fast parallel, schmal mit kräftigem Basalzahn und langem, schmalem Zahn (Abb. 252). Tergit 8 breit (Abb. 253)
 40. *S. s. str. trispinopsis* sp. nov.

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- Fühlerglied 1 fast dreieckig, nicht parallel, der Basalzahn fehlt, der vordere Zahn breit, ausgehöhlt (Abb. 258). Tergit 8 schmal (Abb. 259)
 - 41. *S. s. str. oneili* Pic
- 43. Die beiden Seitenteile von Sternit 8 hängen lose zusammen44
 - Die beiden Seitenteile von Sternit 8 hängen nicht zusammen, sie sind vollständig frei45
- 44. Fühlerglied 1 fast parallel, an der Basis kurz ausgehöhlt, Zahn kaum angedeutet (Abb. 268)
 - 42. *S. s. str. leucosideae* sp. nov.
 - Fühlerglied 1 nicht parallel, an der Basis länglich ausgehöhlt, Zahn sehr klein, deutlich (Abb. 274)
 - 43. *S. s. str. amatolensis* sp. nov.
- 45. Die Aushöhlung an der Basis von Fühlerglied 1 befindet sich vor der Mitte46
 - Die Aushöhlung von Fühlerglied 1 erreicht die Mitte oder überragt sie sogar, an Stelle eines Zahnes ist dieser Teil breit nach unten verlängert (Abb. 280)
 - 44. *S. s. str. nelshoogtensis* sp. nov.
- 46. Zahn von Fühlerglied 1 mehr dreieckig, an der Basis nicht eingeschnürt47
 - Zahn von Fühlerglied 1 nicht dreieckig, nach der Basis eingeschnürt (Abb. 287)
 - 45. *S. s. str. quadratipalpus* sp. nov.
- 47. Zahn von Fühlerglied 1 breiter (Abb. 284)
 - 45. *S. s. str. nelshoogtensis transformatus* ssp. nov.
 - Zahn von Fühlerglied 1 zierlicher (Abb. 293)
 - 47. *S. s. str. trimaculatus* sp. nov.
- 48. Die Fortsätze von Sternit 8 sind nach aussen gebogen49
 - Die Fortsätze von Sternit 8 sind nach innen gebogen und spitz53
- 49. Jeder Seitenteil von Sternit 8 ausser den Fortsätzen am Apex mit einem zusätzlichen spitzen Fortsatz auf der Innenseite50
 - Jeder Seitenteil von Sternit 8 ohne zusätzlichen spitzen Fortsatz auf der Innenseite51
- 50. Der zusätzliche Fortsatz von Sternit 8 auf der Innenseite ist sehr lang, an der Basis sehr breit (Abb. 302)
 - 48. *S. s. str. tridensmimus* sp. nov.
 - Der zusätzliche Fortsatz von Sternit 8 ist auf der Innenseite sehr kurz, an der Basis schmal, dornförmig (Abb. 308)
 - 49. *S. s. str. longidens* Champion
- 51. Fühlerglied 1 an der Basis ohne zusätzlichen Zahn52
 - Fühlerglied 1 an der Basis mit einem breiten zusätzlichen Zahn (Abb. 313)
 - 50. *S. s. str. bidens* Champion
- 52. Zahn auf Fühlerglied 1 gross, er bildet einen schwachen spitzen Winkel (Abb. 321)
 - 51. *S. s. str. dwesaensis* sp. nov.

- Zahn auf Fühlerglied 1 nicht spitz, sondern breit gerundet, nur an der Basis befindet sich eine kurze Spitze (Abb. 327)
52. *S. s. str. nigriceps* sp. nov.
- 53. Sternit 8 ohne lange, nach innen gerichtete Borsten54
– Sternit 8 mit 1 oder 2 langen, nach innen gerichteten Borsten64
- 54. Sternit 8 ohne langen, nach hinten gerichteten Fortsatz55
– Sternit 8 mit langem, nach hinten gerichtetem, spitzem Fortsatz, der fast parallel mit dem Seitenteil verläuft (Abb. 335)
53. *S. s. str. uitsoekensis* sp. nov.
- 55. Sternit 8 zur Spitze nicht verbreitert, dahinter nicht eingeschnürt57
– Sternit 8 zur Spitze verbreitert, dahinter eingeschnürt56
- 56. Apikaler Teil von Sternit 8 fast parallelseitig, dann jederseits mit einem dorsalwärts gerichteten, leicht gekrümmten, spitzen Fortsatz (Abb. 340)
54. *S. s. str. curvispinus* sp. nov.
– Apikaler Teil von Sternit 8 nicht fast parallel, sondern zur Spitze verbreitert, ohne dorsal gerichteten spitzen Fortsatz (Abb. 346)
55. *S. s. str. acutispinus* sp. nov.
- 57. Sternit 8 nicht leierförmig geformt61
– Sternit 8 fast leierförmig (Abb. 352, 363, 369) 58
- 58. Glied 3 der Maxillarpalpen 2 mal so lang oder noch länger als der Vorderrand dieses Gliedes59
– Glied 3 der Maxillarpalpen weniger als 2 mal so lang wie der Vorderrand dieses Gliedes60
- 59. Glied 2 der Maxillarpalpen eine breite Lamelle mit fast geradem Distalrand (Abb. 348)
56. *S. s. str. majeri* sp. nov.
– Glied 2 der Maxillarpalpen distal nicht breit, das Glied ist schmal, etwas gebogen (Abb. 356)
57. *S. s. str. expansus* sp. nov.
- 60. Glied 3 der Maxillarpalpen apikal kaum verschmälert, breit gerundet (Abb. 359)
58. *S. s. str. oculimaculatus* sp. nov.
– Glied 3 der Maxillarpalpen apikal verschmälert, ausgerandet (Abb. 365)
59. *S. s. str. zulu* sp. nov.
- 61. Die beiden Seitenteile von Sternit 8 hängen in der Mitte nicht lose zusammen, sie sind vollständig getrennt. Tergit 8 apikal in der Mitte spitz vorstehend62
– Die beiden Seitenteile von Sternit 8 hängen in der Mitte zusammen (Abb. 375). Tergit 8 apikal gerundet
60. *S. s. str. politus* sp. nov.
- 62. Spitzen von Sternit 8 stark nach innen gebogen63
– Spitzen von Sternit 8 schwach nach innen gebogen (Abb. 382)
61. *S. s. str. levemaculatus* sp. nov.

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63. Fühlerglied 3 ein wenig verbreitert (Abb. 386). Die nach innen gerichteten Spitzen von Sternit 8 befinden sich kurz vor der Spitze (Abb. 388)
62. *S. s. str. trispinus* sp. nov.
- Fühlerglied 3 nicht verbreitert (Abb. 392). Die nach innen gerichteten Spitzen von Sternit 8 beginnen an der Spitze (Abb. 394)
63. *S. s. str. productus* sp. nov.
64. Sternit 8 jederseits mit 1 langen nach innen gerichteten Borste65
– Sternit 8 jederseits mit 2 langen nach innen gerichteten Borsten, öfters erscheinen diese beiden Borsten wie zusammengeklebt68
65. Die beiden Seitenteile von Sternit 8 sind miteinander durch loses Gewebe verbunden66
– Die beiden Seitenteile von Sternit 8 sind vollständig getrennt67
66. Fühlerglied 1 bis ungefähr zur Mitte tief ausgehöhlt (Abb. 398). Tergit 8 apikal gerundet mit einem kleinen Fortsatz in der Mitte (Abb. 399)
64. *S. s. str. rudebecki* sp. nov.
- Fühlerglied 1 nur an der Basis kurz ausgehöhlt (Abb. 405). Tergit 8 apikal in Wellenlinie, in der Mitte ein wenig mehr vorstehend als an der Seiten (Abb. 406)
65. *S. s. str. wezaensis* sp. nov.
67. Fühlerglied 1 fast dreieckig mit einem grossen, langen Zahn in der Mitte und einem viel kleineren an der Basis (Abb. 411)
66. *S. s. str. dentatus* sp. nov.
- Fühlerglied 1 länglich, nicht dreieckig, mit nur 1 Zahn nach der Aushöhlung (Abb. 418)
67. *S. s. str. bedfordensis* sp. nov.
68. Fühlerglied 1 vor dem Zahn ein wenig ausgehöhlt, aber an der Basis nicht verdickt69
– Fühlerglied 1 an der Basis verdickt und hier manchmal mit 1 Zahn70
69. Fühlerglied 1 fast parallel, Aushöhlung klein, Zahn kaum angedeutet (Abb. 424). Tergit 8 apikal in der Mitte stumpfwinklig vorstehend (Abb. 425)
68. *S. s. str. zimbabwensis* sp. nov.
- Fühlerglied 1 länglich dreieckig mit kräftigem Zahn (Abb. 430). Tergit 8 apikal regelmässig gerundet (Abb. 431)
69. *S. s. str. basutolandicus* sp. nov.
70. Fühlerglied 1 an der Basis mit 1 Zahn oder mit 1 stumpfen Höcker71
– Fühlerglied 1 an der Basis ohne Zahn oder Höcker, hier nur ausgehöhlt, diese Stelle einen stumpfen Winkel bildend (Abb. 436)
70. *S. s. str. breytenbachae* sp. nov.
71. Fühlerglied 1 mit einem Zahn an der Basis72
– Fühlerglied 1 mit einem Höcker an der Basis, Zahn besonders lang, etwas verdreht (Abb. 442)
71. *S. s. str. elongatidens* sp. nov.

72. Fühlerglied 1 an der breitesten Stelle spitz vorstehend73
 – Fühlerglied 1 an der breitesten Stelle einen leicht stumpfen Winkel bildend (Abb. 448)
 72. *S. s. str. karkloofensis* sp. nov.
73. Die beiden Seitenteile von Sternit 8 sind getrennt (Abb. 455). Fühlerglied 1 mit einer kurzen Querleiste neben der Aushöhlung (Abb. 453)
 73. *S. s. str. nylsvleyensis* sp. nov.
- Die beiden Seitenteile von Sternit 8 hängen zusammen (Abb. 460). Fühlerglied 1 mit einem kleinen zusätzlichen Zahn neben der Aushöhlung (Abb. 458)
 74. *S. s. str. tridens* sp. nov.

BESCHREIBUNGEN (TAXONOMIE) UND KOMMENTARE

1. *Sphinginopalpus (Sphinginafricanus) atripennis* Champion

Abb. 1-8

Sphinginopalpus atripennis Champion, 1922: 333.

Für die Abb. 1 und 2 der Maxillarpalpen diente der Holotypus im BM and für die Abb. 3-7 ein ♂ von Badplaas. Fühlerglieder 1 bis 4 Abb. 3. Tergit 8 Abb. 4. Sternite 7 und 8 Abb. 5 und 6. Kopulationsapparat Abb.7.

Die Art ist auffällig durch das einfache, ungezahnte Fühlerglied 1 beim ♂. Die ♂ kommen geflügelt und ungeflügelt vor. Die geflügelten ♂ besitzen normal entwickelte Schulterbeulen, bei den ungeflügelten Exemplaren treten die Schultern spitz vor. Die Art ist weit verbreitet.



1



2

Abb. 1-2. *Sphinginopalpus (Sphinginafricanus) atripennis* Champion ♂: 1-2, Maxillarpalpen (x220) (1 von oben, 2 von unten).

UNTERSUCHTES MATERIAL: Natal: St Lucia, 10 m, 23-25.x.1981 (J. & S. Klapperich) (NHMB). Transvaal: Waterval Boven, 24.xi.1981 (J. & S. Klapperich) (NHMB); Nelspruit Nat. Res., groundtraps banana bait and grass netting, 23.ix. & 19.xii.1986, E-Y:2287, 2402 (S. Endrödy- Younga) (TMP); 16 km N Barberton, 25°42' S, 30°57' E, 24.ix.1986 and 10.ii.1987, ground traps banana bait, E-Y:2287 & 2438 (S. Endrödy- Younga) (TMP & NHMB); Berlin Forest Station, 1500 m, 7.xii.1986, E-Y:2360 (S. Endrödy-Younga) (TMP & NHMB); Uitsoek Forest Station, 1100 m,

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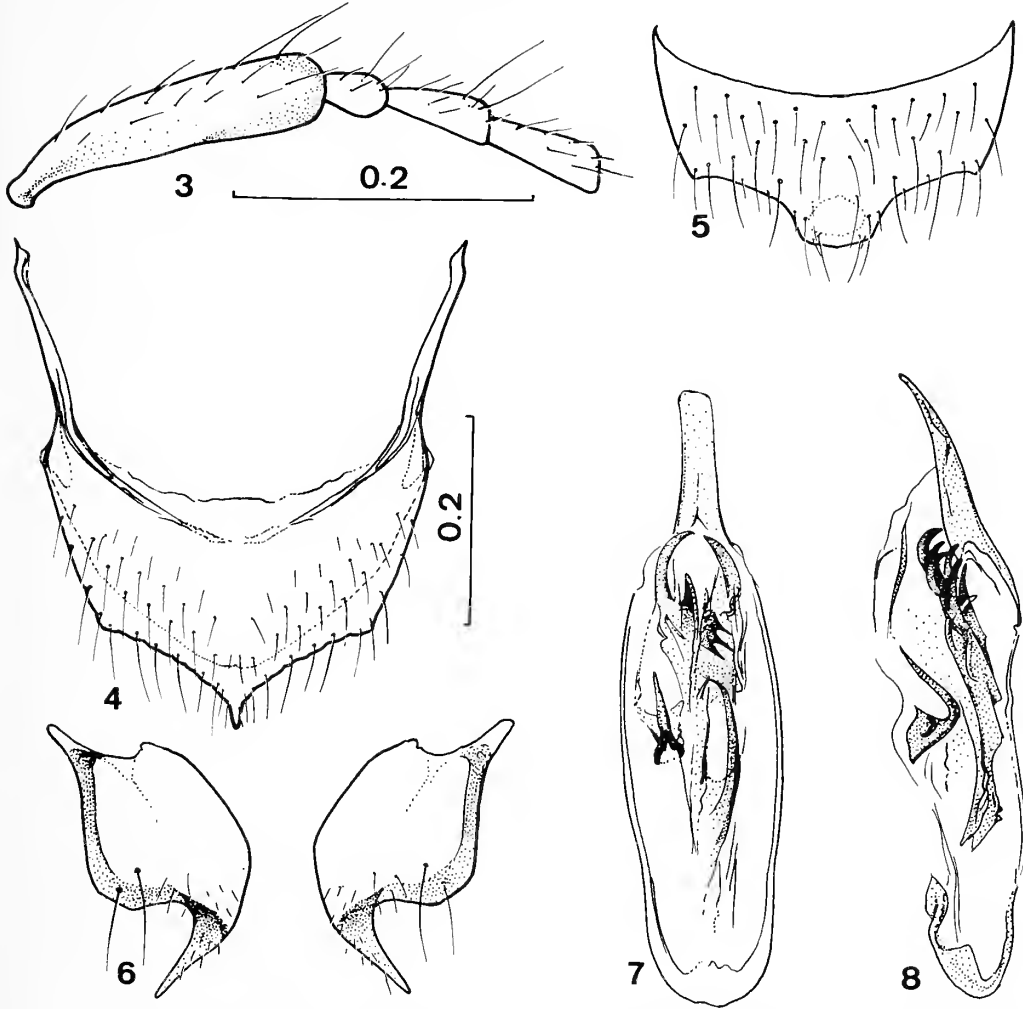


Abb. 3-8. *Sphinginopalpus (Sphinginafricanus) atripennis* Champion ♂: 3, Fühlerglieder 1-4; 4, Tergit 8; 5, Sternit 7; 6, Sternit 8; 7-8, Kopulationsapparat (7, dorsal; 8, Profil). Massstab von 4 auch für 5-8.

12.xii.1986, E-Y:2379 (S. Endrödy-Younga) (TMP); Nelshoogte Devil's Knuckles, grass netting,
 4.xii.1986, E-Y:2350 (S. Endrödy-Younga) (TMP); Nelshoogte Forest Station, grass netting,
 1.xii.1986, E-Y:2336 (S. Endrödy-Younga) (TMP); Soutpansberg Hanglip, 23°02'S, 29°47'E, grass
 netting, 14.iii.1973, E-Y:46 (S. Endrödy-Younga) (TMP). Transkei: Fraser Gorge, grass tussocks,
 31°24'S, 29°42'E,
 E-Y:2584 (S. Endrödy-Younga) (TMP). Zululand: Lake Bhangasi, grass netting, 28°07'S, 32°31'E,
 18.xii.1976 (S. Endrödy-Younga) (TMP).

2. *Sphinginopalpus (Sphinginafricanus) pallidicornis* sp. nov.

MÄNNCHEN (Abb. 9-14).

Länge 1,8 - 2 mm.

Kopf schwarz, Vorderkopf mit einem mehr oder weniger grossen gelben Flecken, der bis zur Mitte der Augen reichen kann, ohne sie zu berühren, manchmal auch ein Teil der Wangen hell; Maxillarpalpen orange, Oberseite des vorletzten Gliedes dunkelbraun, Spitze des letzten sehr oft schwach gebräunt; Fühler orange, Spitze des letzten Gliedes oft leicht angedunkelt; Halsschild schwarz, abgeflachter Teil an der Basis orange; Schildchen orange; Flügeldecken schwarz, Seiten beginnend an der Basis bis und mit Spitzen schmal gelb; Hinterschenkel schwarz, Basis breit aufgehellt, Hintertibien an der Basis schmal hell, alle Tarsen orange, 4 Vorderbeine orange, jedoch Schenkel teils angedunkelt.



Abb. 9-10. *Sphinginopalpus (Sphinginafricanus) pallidicornis* sp. nov. ♂: 9-10, Maxillarpalpen (x200) (9, von oben; 10, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 9-10. Fühler (Abb. 11) auffällig durch das ungezähnte Glied 1, 3 nur wenig länger als 4. Halsschild länger als breit (17x14); Oberfläche glatt, auf dem basalen Teil neben dem Seitenrand schmal chagriniert, der Seitenrand hier schwach krenuliert, Flügeldecken oval, Schulterbeulen schwach gerundet oder spitz vortretend; falsche Epipleuren nur ganz schwach krenuliert; Punktreihen deutlich, Punkte erst nach der Mitte an Tiefe verlierend, Spitze fast unpunktiert. Tergit 8 Abb. 12. Sternit 7 Abb. 13, Sternit 8 Abb. 14.

WEIBCHEN.

Wie das ♂ gefärbt, nur Kopf und Maxillarpalpen einfarbig schwarz. Schulterbeulen spitz vortretend.

Holotypus ♂ und 4 Paratypen (NHMB), 2 Paratypen ♂ ♀ (TMP), 2 Paratypen ♂ ♀ (AMG): South Africa, Natal: 7 km NO Ladysmith, 21.xi.1987 (W. Wittmer).

Neben *S. (S.) atripennis* Champion zu stellen. Die neue Art unterscheidet sich durch die hellen Fühler und die gelben Seiten der Flügeldecken, sowie durch die verschieden gebauten Terminalia. Es ist bis jetzt die einzige Art dieser Untergattung deren Tergit 8 in drei Spitzen ausläuft, sie hat

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deshalb grosse Ähnlichkeit mit *S. s. str. flavomarginatus* Champion, doch ist das Sternit 8 verschieden gebaut.

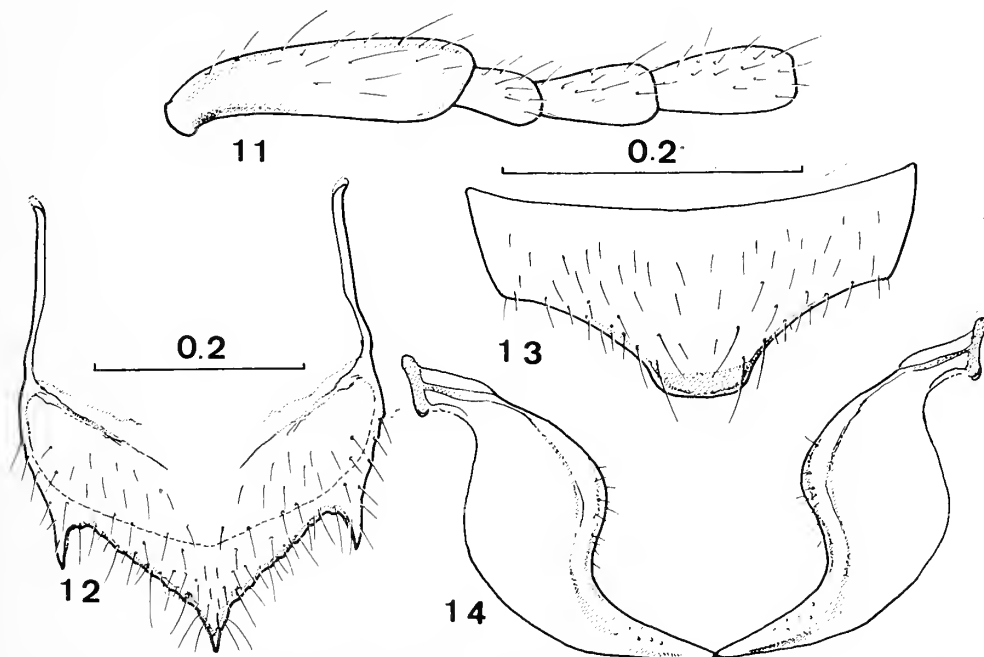


Abb. 11-14. *Sphinginopalpus (Sphinginafricanus) pallidicornis* sp. nov. ♂: 11, Fühlerglieder 1-4; 12, Tergit 8; 13, Sternit 7; 14, Sternit 8. Massstab von 11 auch für 14 und 12 auch für 13.

3. *Sphinginopalpus (Sphinginafricanus) delicatulus* sp. nov.

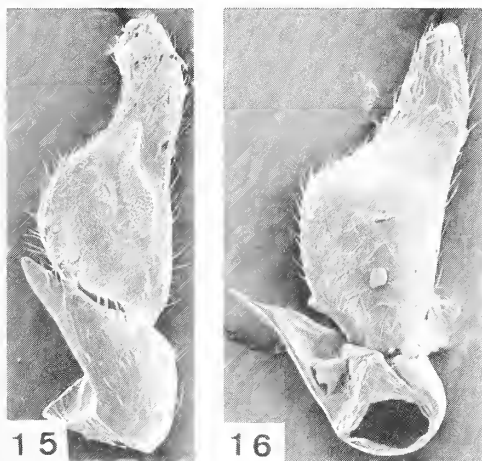


Abb. 15-16. *Sphinginopalpus (Sphinginafricanus) delicatulus* sp. nov. ♂: 15-16, Maxillarpalpen (x200).

MANNCHE (Abb. 15-21).

Länge 2,2 mm.

Kopf schwarz; Maxillarpalpen gelb, Spitze des letzten Gliedes schmal angedunkelt; Fühler gelb, letzte 3 bis 4 Glieder dunkel; aufgewölbter Teil des Halsschildes schwarz, abgeflachte Basis gelblich; Schildchen, Flügeldecken und Hinterbeine schwarz, Hintertarsen leicht aufgehellt, 4 Vorderbeine und Tarsen gelb, Schenkel teils angedunkelt.

Kopf mit Augen breiter als der Halsschild, Stirne leicht gewölbt, Oberfläche glatt. Maxillarpalpen (Abb. 15-16) besonders schlank, letztes Glied apikal zugespitzt. Fühler (Abb. 17) mit Glied 1 einfach (ungezähnt), 3 kaum merklich länger als 4. Halsschild länger als breit (16x13,5), Seiten

von der Mitte an schwach gerundet; Oberfläche glatt, nur neben dem Seitenrand an der Basis des abgeflachten Teils auf kurzer Strecke runzlig gewirkt. Flügeldecken langoval, Schulterbeulen normal; Punkte in den Reihen ziemlich tief, nicht ganz regelmässig; falsche Epipleuren ca. 45% der Länge einnehmend, nicht krenuliert; geflügelt. Tergit 8 Abb. 18. Sternit 8 Abb. 19.

Kopulationsapparat Abb. 20 dorsal, Abb. 21 Profil.

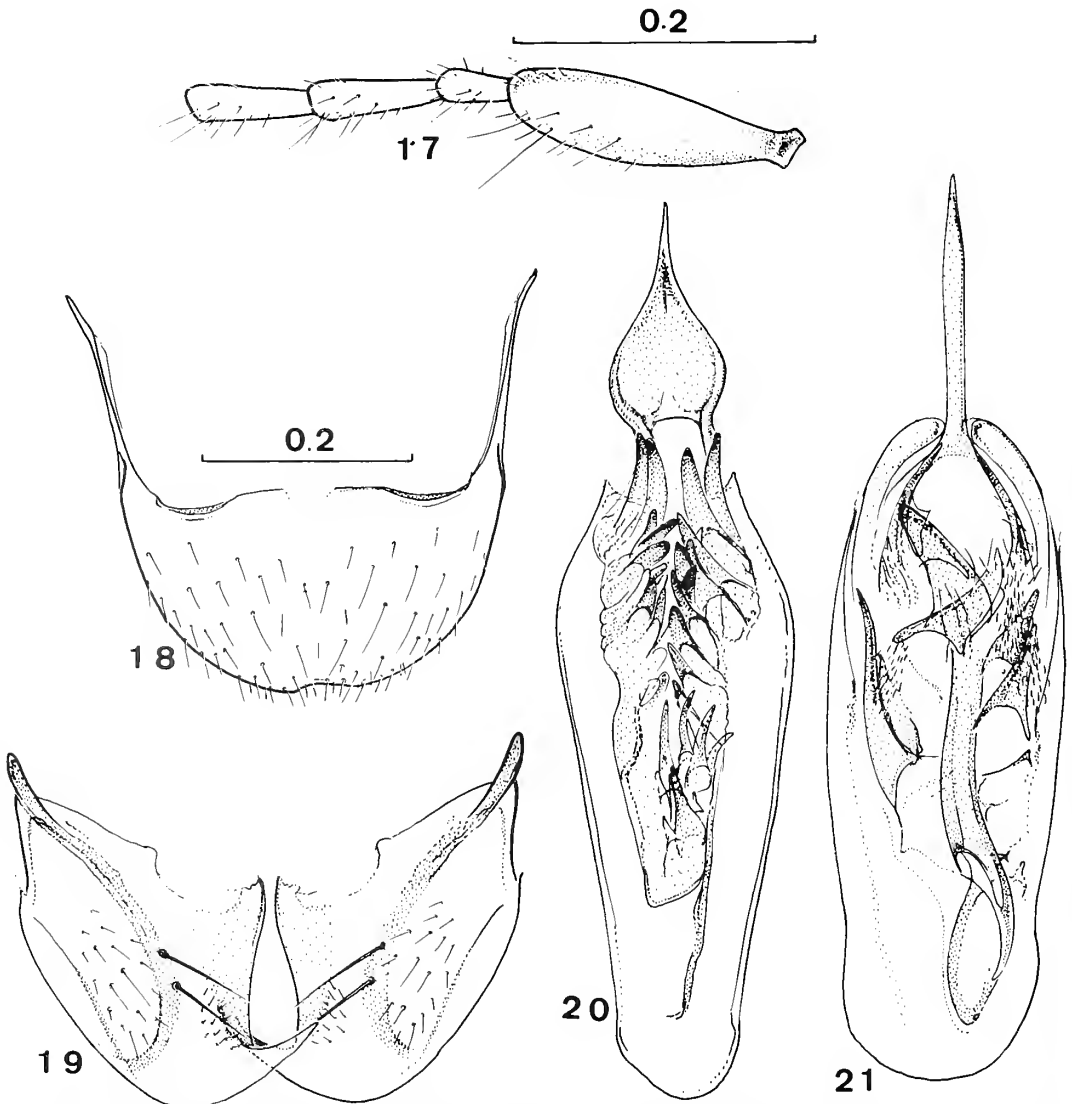


Abb. 17-21. *Sphinginopalpus (Sphinginafricanus) delicatulus* sp. nov. ♂: 17, Fühlerglieder 1-4; 18, Tergit 8; 19, Sternit 8; 20-21, Kopulationsapparat (20, dorsal; 21, Profil). Massstab von 17 auch für 19-21.

WEIBCHEN unbekannt.

Holotypus (TMP): South Africa, E. Transvaal: Nelshoogte Forest Station, 1400 m, grassnetting, 2.xii.1986, E-Y:2345, S. Endrödy- Younga.

Obwohl von dieser Art keine ♀ vorliegen, stelle ich sie in die Untergattung *Sphinginafricanus*, weil sie so nahe mit *atripennis* Champion verwandt ist. Sie unterscheidet sich von ihr durch die sehr schmalen Maxillarpalpen, die Terminalia und den Kopulationsapparat.

4. *Sphinginopalpus (Sphinginafricanus) bilineaticeps* Pic

Sphinginopalpus bilineaticeps Pic, 1929: 2.

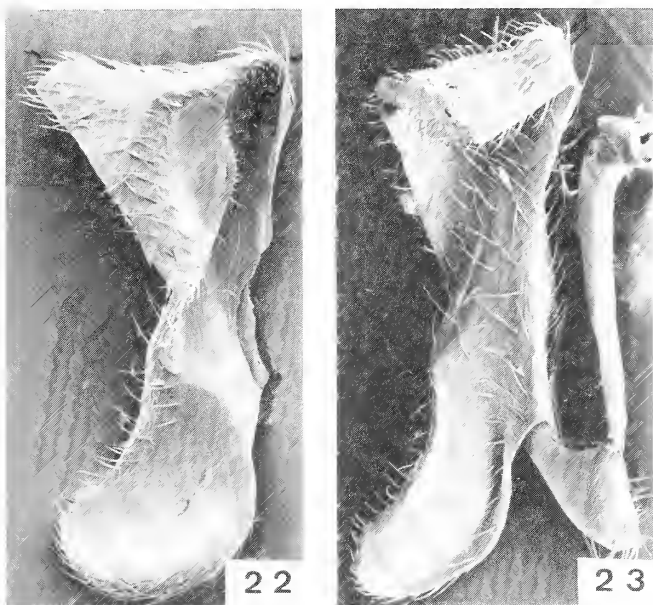


Abb. 22-23. *Sphinginopalpus (Sphinginafricanus) bilineaticeps* Pic ♂: 22-23, Maxillarpalpen (x165).

MANNCHEN (Abb. 22-27).

Der Holotypus befindet sich im BM. Schon durch die Färbung des Kopfes fällt diese Art auf. Die Kopfbasis ist schwarz, von der Mitte der Augen nach vorne gelb, über jeder Fühlerwurzel ein kleiner schwarzer, länglicher Flecken. Die beigegebenen Abbildungen werden ein Erkennen erleichtern: Maxillarpalpen Abb. 22-23. Tergit 8 (Abb. 25) sehr charakteristisch durch den schmalen, in der Mitte vorstehenden Apikalrand, der fast bis zur Basis eingeschnitten ist. Sternit 8 Abb. 26. Kopulationsapparat Abb. 27 dorsal.

Die Art ist aus Natal beschrieben: Weenen, xii.1923, H. P. Thomasset. Ein weiteres ♂ wurde von mir ebenfalls in Natal erbeutet: 4 km S Wasbank, R621,

1030 m, 21.xi.1987 (NHMB). Dieses Exemplar unterscheidet sich von der Holotype lediglich durch das etwas stärker verbreiterte Fühlerglied 5. Dann fing Dr. S. Endrödy- Younga (E-Y:2787) 1 ♂ in Karkloof grassveld, 29°19'S, 30°15'E (TMP).

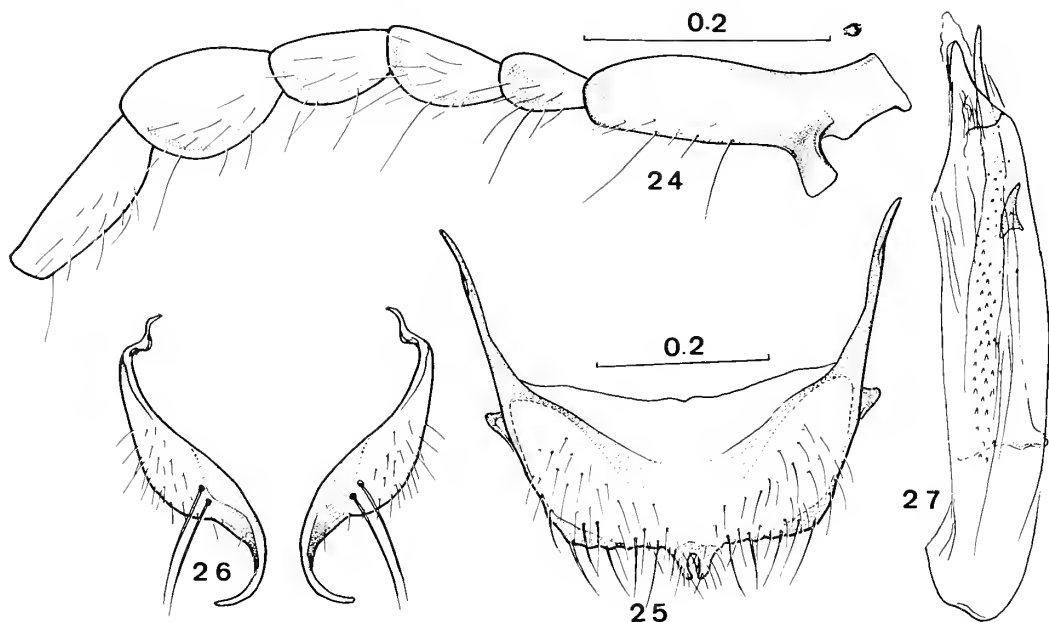


Abb. 24-27. *Sphinginopalpus (Sphinginafricanus) bilineaticeps* Pic ♂: 24, Fühlerglieder 1-6; 25, Tergit 8; 26, Sternit 8; 27, Kopulationsapparat (dorsal). Massstab von 25 auch für 26, 27.

5. *Sphinginopalpus (Sphinginafricanus) reavelli* sp. nov.

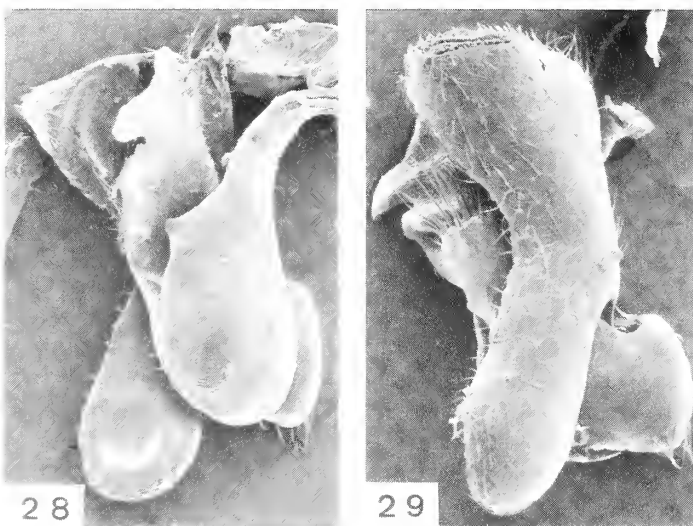


Abb. 28-29. *Sphinginopalpus (Sphinginafricanus) reavelli* sp. nov. ♂: 28-29, Maxillarpalpen (x130) (28, von oben; 29, von unten).

MANNCHE (Abb. 28-33).

Länge 2,5-2,7 mm.

Kopf gelb bis orange, Stirne mit einem mehr oder weniger blassen, dunkeln Flecken, der bis zur Mitte der Augen reicht, Schläfen hell; Maxillarpalpen hellbraun, oft mit 1 bis 2 kleinen dunkeln Flecken; Fühler gelb, Glieder 3 bis 5 oder 6 dunkel, Oberseite von 2 meistens angedunkelt. Halsschild schwärzlich bis mehr oder weniger dunkel braun, Basis orange bis hellbraun; Schildchen und Flügeldecken schwarz, falsche Epipleuren mit schwacher

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

Tendenz zu Aufhellung; Hinterbeine schwarz, Hintertibien teils aufgehellt, oder ganz gelb, Mittelschenkel dunkel, meistens ein wenig aufgehellt, Mitteltibien schwarz bis schwärzlich, Mitteltarsen gelb, Vorderschenkel und Vordertibien noch heller als die mittleren; alle Trochanteren und Spitzen der Koxen gelb.

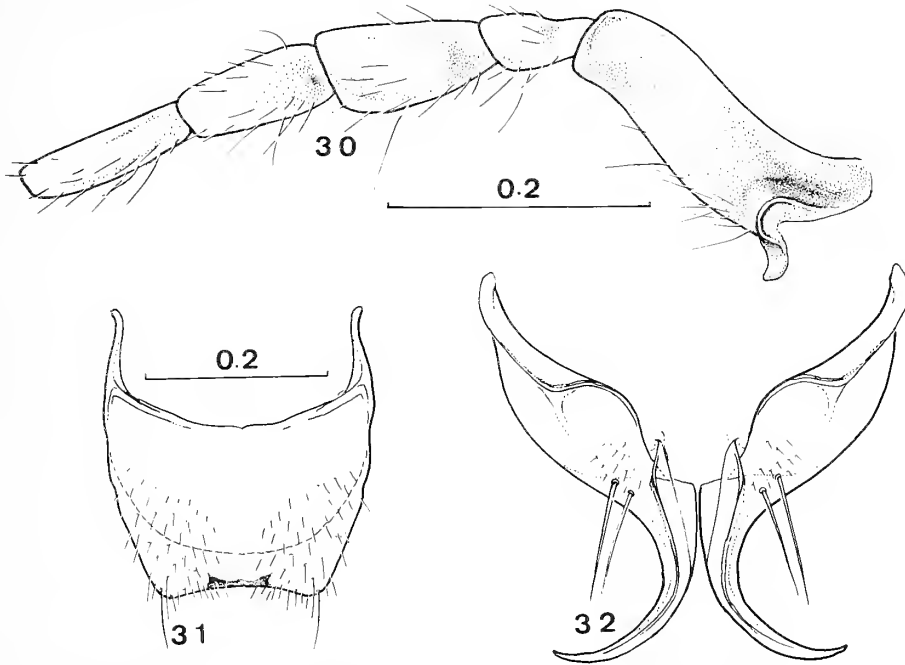


Abb. 30-33. *Sphinginopalpus (Sphinginafricanus) reavelli* sp. nov. ♂: 30, Fühlerglieder 1-5; 31, Tergit 8; 32, Sternit 8; 33, Kopulationsapparat (Profil). Massstab von 30 auch für 32, 33.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 28 von oben, Abb. 29 von unten. Fühler (Abb. 30) um etwas mehr als 1/10 länger als die Flügeldecken, Zahn auf Glied 1 deutlich gebogen, 3 und 4 abgeflacht, beide fast gleich lang, 3 breiter als 4. Halsschild länger als breit (22x15), sonst wie bei *curvipalpis*; Oberfläche regelmässig chagriniert. Flügeldecken wie bei *curvipalpis*, Punkte weniger tief. Tergit 8 Abb. 31. Sternit 8 Abb. 32.

Kopulationsapparat Abb. 33 Profil.

WEIBCHEN.

Kopf einfarbig schwarz, Fühler einfarbig gelb, beim Halsschild ist auch der dunkle Teil dunkler als beim ♂, Beine dunkler als beim ♂. Fühlerglied 12 schmal, zur Spitze wenig verbreitert, übrige Glieder fast parallel. Flügeldecken breiter als beim ♂; ungeflügelt.

Holotypus und 2 Paratypen (NHMB): South Africa, Natal: Grass edge at Glinza Forest, Eshowe, 19.xii.1985, P. E. Reavell; idem 1 Paratypus (NCl); idem 25.iv.1956, H. K. Munro, 1 Paratypus

(NCI); idem 23.- 31.iii., 1.- 22.iv., 23.- 30.iv.1926, R. E. Turner, 5 ♀ Paratypen (BM), 3 ♀ Paratypen (NHMB).

Diese neue Art gehört zu den wenigen mit verbreiterten Fühlergliedern und ist neben *bilineaticeps* Pic zu stellen. Sie unterscheidet sich von dieser Art durch die verbreiterten Fühlerglieder 3 und 4, währendem bei *bilineaticeps* die Glieder 3 bis 5 verbreitert sind. Weitere Unterschiede zeigen die Maxillarpalpen, die Terminalia und der Kopulationsapparat.

6. *Sphinginopalpus (Sphinginafricanus) complicatus* sp. nov.

MÄNNCHEN (Abb. 34-39).



Länge 2,5 mm.

Kopf schwarz, von der Mitte der Augen nach vorne gelb; Maxillarpalpen schwarz; Fühlerglieder 1 bis 5 gelb, 1 auf der Oberseite und an der Basis kurz dunkel, 6 und folgende zunehmend dunkel; Halsschild schwarz, Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere seitlich schmal mit Tendenz zu Aufhellung; Hinterschenkel und grösster Teil der Hinterschienen schwarz, Hintertarsen gelb mit den beiden Basalgliedern schwach dunkel; Mittelschenkel und Mittelschienen angedunkelt, Vorderschenkel auf der basalen Hälfte dunkel, Rest mit den Schienen gelb, 4 Vordertarsen gelb.

Abb. 34-35. *Sphinginopalpus (Sphinginafricanus) complicatus* sp. nov.
♂: 34-35, Maxillarpalpen (x130) (34, von oben; 35, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt, Oberfläche fein chagriniert. Maxillarpalpen Abb. 34-35. Fühler (Abb. 36) ein wenig kürzer als die Flügeldecken, Glied 2 fast so lang wie 3, 4 so lang wie 3, 3 bis 10 fast parallel. Halsschild ungefähr in der Mitte an breitesten; Oberfläche fein chagriniert, sonst wie bei *curvipalpis*. Flügeldecken wie bei *curvipalpis*, Punktierung etwas weniger tief, in Reihen angeordnet. Tergit 8 Abb. 37. Sternit 8 (Abb. 38) mit sichelförmigen Verlängerungen, die übereinander greifen.

Kopulationsapparat Abb. 39 dorsal.

Holotypus und 9 Paratypen (NHMB), 2 Paratypen (AMG): South Africa, Transvaal: Blydepoort, 20.xi.1981, J. & S. Klapperich.

Wegen dem sehr abweichenden Sternit 8 mit keiner anderen Art vergleichbar. Am ehesten noch neben *curvipalpis* Wittmer zu stellen, bei dem das Sternit 8 kurze Ansätze einer Verlängerung der Spitzen nach aussen aufweist.

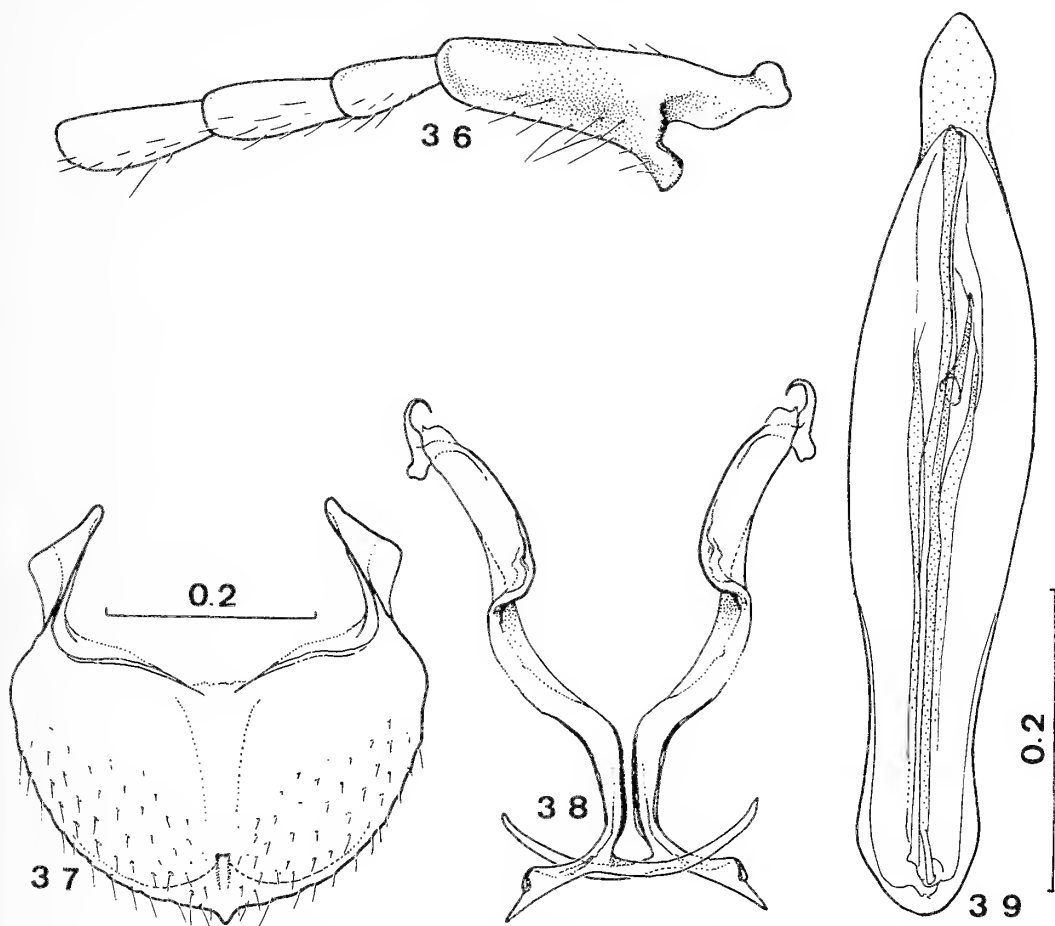


Abb. 36-39. *Sphinginopalpus (Sphinginafricanus) complicatus* sp. nov. ♂: 36, Fühlerglieder 1-4; 37, Tergit 8; 38, Sternit 8; 39, Kopulationsapparat (dorsal). Massstab von 39 auch für 36, 38.

7. *Sphinginopalpus (Sphinginafricanus) nerinaensis* sp. nov.

MÄNNCHEN (Abb. 40-46).

Länge 2,5 mm.

Kopf schwarz, von der Mitte der Augen nach vorne, inklusive der Wangen gelb; Maxillarpalpen gelb; Fühler angedunkelt, erste 4 bis 5 Glieder gelb, 1 auf der Oberseite angedunkelt; Halsschild schwarz, Basis nicht sehr breit hell; Schildchen, Flügeldecken und Beine schwarz, bei den 4 vorderen schwache Tendenz zu Aufhellung.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 40-41. Fühler (Abb. 42) ca. 10% kürzer als die Flügeldecken, Glied 1 nicht

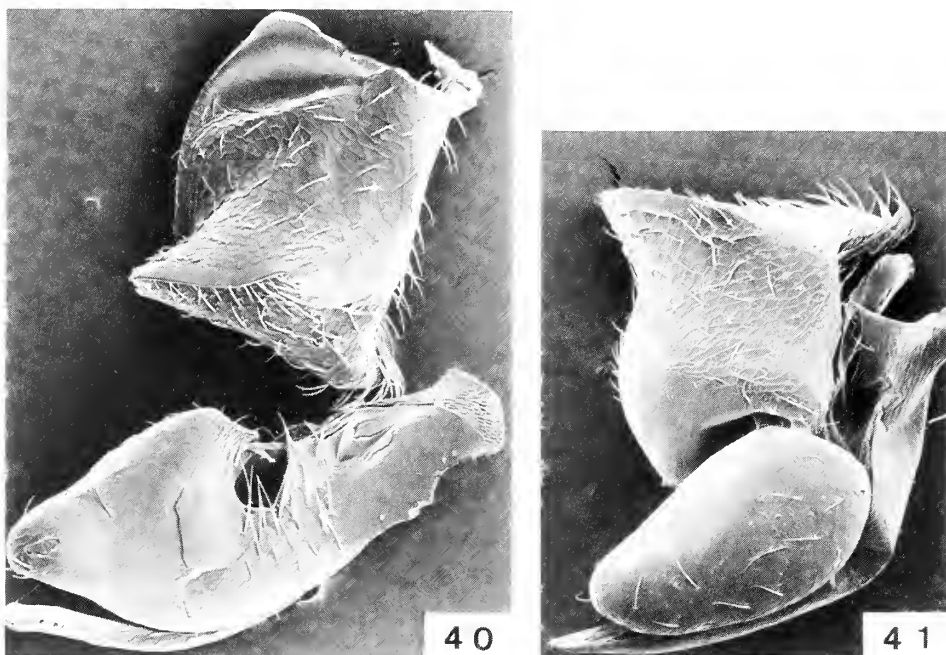


Abb. 40-41. *Sphinginopalpus (Sphinginafricanus) nerinaensis* sp. nov. ♂: 40-41, Maxillarpalpen (x155) (40, von oben, Glied 3 von den übrigen getrennt und verkehrt liegend; 41, von unten).

ausgerandet, fast auf der Unterseite und erst nach der Mitte gelegen ein spitzer Zahn, 3 nur wenig länger als 4. Halsschild länger als breit (25x17), Seiten bis zur Hälfte fast parallel, dann verengt, sonst wie *curvipalpis*. Flügeldecken wie bei *curvipalpis*, jedoch Punktierung schwächer, falsche Epipleuren deutlich krenuliert. Tergit 8 Abb. 43. Sternit 8 Abb. 44. Spiculum Abb. 45.

Kopulationsapparat Abb. 46 Profil.

WEIBCHEN.

Kopf einfarbig schwarz, sonst wie das ♂ gefärbt; Fühlerglied 1 sehr lang und schmal; Schulterbeulen durch eine schwache Erhöhung kaum angedeutet; ungeflügelt.

Holotypus ♂ und 1 Paratypus ♀ (TMP): South Africa, Transvaal: Nerina Nature Reserve, 23°42'S, 30°16'E, 22.iii.1975, E-Y:761, S. Endrödy-Younga.

Neben *reavelli* Wittmer zu stellen, jedoch ohne verbreiterte Fühlerglieder und sehr verschieden gebaute Terminalia.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

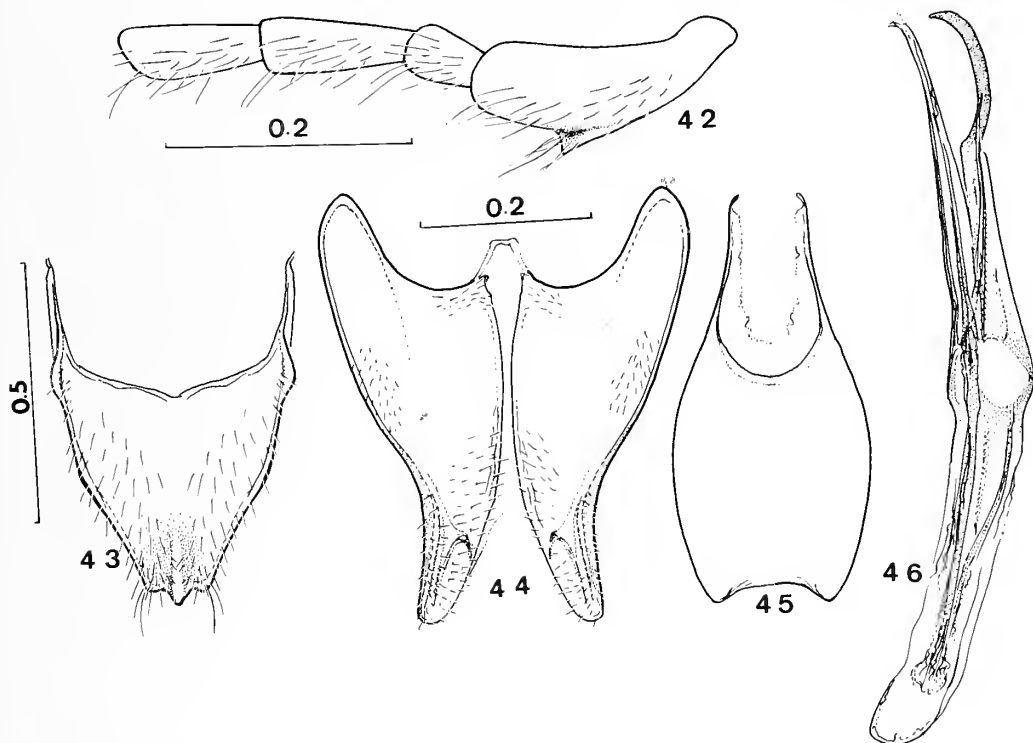


Abb. 42-46. *Sphinginopalpus (Sphinginafricanus) nerinaensis* sp. nov. ♂: 42, Fühlerglieder 1-4; 43, Tergit 8; 44, Sternit 8; 45, Spiculum; 46, Kopulationsapparat (Profil). Massstab von 44 auch für 45, 46.

8. *Sphinginopalpus (Sphinginafricanus) endroedyi* sp. nov.

MÄNNCHEN (Abb. 47-53).

Länge 2,2 - 2,3 mm (ohne Abdomen).

Kopf orange bis gelb, ein schwarzer Stirnflecken reicht bis zur Mitte der Augen und bedeckt meistens auch die Schläfen; Maxillarpalpen orange, bei 1 Exemplar braun; Fühler gelb, die letzten 4 bis 5 Glieder dunkel; Halsschild schwarz, abgeflachte Basis orange; Schildchen und Flügeldecken schwarz, letztere mit einem gelben Seitenband, das von der Basis bis fast zu den Spitzen reicht; Hinterbeine schwarz, manchmal sind die Hintertibien leicht aufgehell, Hintertarsen gelb, 4 vordere Beine gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 47-48. Fühler (Abb. 49), Glied 2 verhältnismässig lang, 3 so lang wie 4. Halsschild länger als breit (19x14), Seiten nach vorne leicht gerundet verengt, gegen die Basis verengt, Seitenrand deutlich, Oberfläche auf dem abgeflachten Teil zwischen der kurzen, seitlichen Längsleiste und dem Seitenrand chagriniert, Rest glatt. Flügeldecken oval; Schulterbeulen als kleine Beulen vortretend, auf der eine lange Borste sitzt; falsche Epipleuren nur ganz schwach krenuliert; Punkte

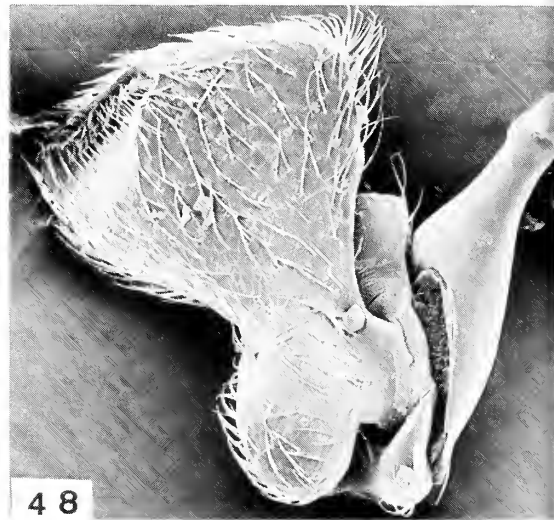
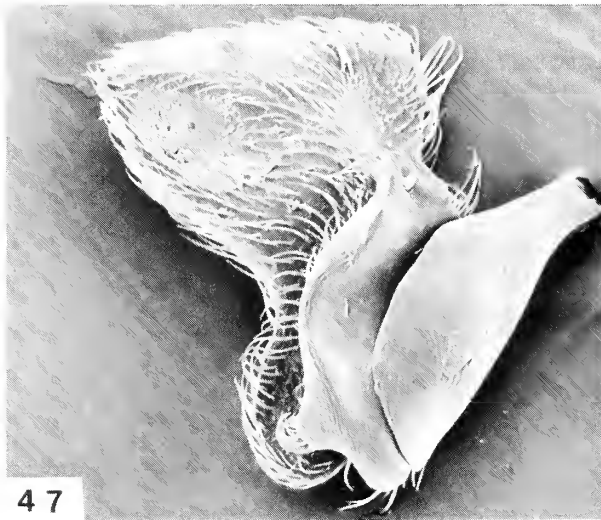


Abb. 47-48. *Sphinginopalpus (Sphinginafricanus) endroedyi* sp. nov. ♂: Maxillarpalpen (x200) (47, von oben; 48, von unten).

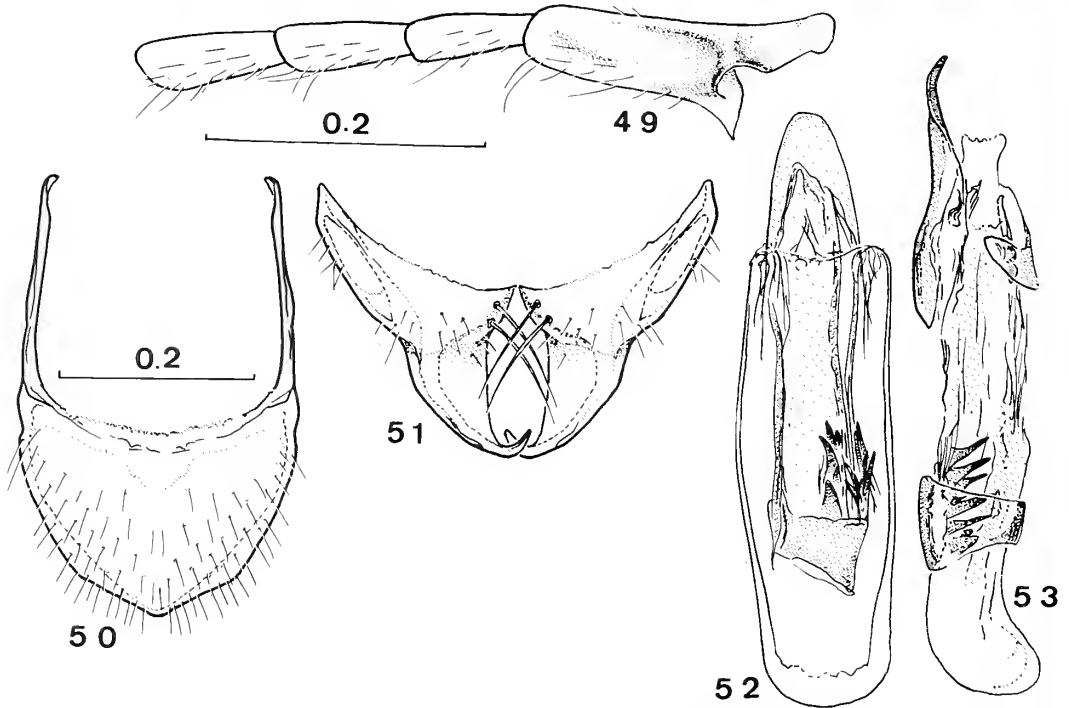


Abb. 49-53. *Sphinginopalpus (Sphinginafricanus) endroedyi* sp. nov. ♂: 49, Fühlerglieder 1-4; 50, Tergit 8; 51, Sternit 8; 52-53, Kopulationsapparat (52, dorsal; 53, Profil). Massstab von 50 auch für 51-53.

bis etwas über die Mitte in regelmässigen Reihen angeordnet, dann etwas verworren und an Tiefe abnehmend; ungeflügelt. Tergit 8 Abb. 50. Sternit 8 Abb. 51.

Kopulationsapparat Abb. 52 dorsal, Abb. 53 Profil.

WEIBCHEN.

Kopf einfarbig schwarz, an den Fühlern sind die letzten Glieder manchmal leicht angedunkelt, sonst wie das ♂ gefärbt.

Holotypus ♂ and 8 Paratypen (TMP), 5 Paratypen (NHMB), 1 Paratypus (AMG): South Africa, S Natal: Impetyene grassveld, Weza, 25.xi.1989, 30°37'S, 29°42'E, E-Y:2717, S. Endrödy-Younga; E Transvaal: Nelshoogte Forest Station, grassnetting, Knuckles rock forest, 1.xii.1986, 25°47'S, 30°50'E, E-Y:2338, S. Endrödy-Younga, 4 Paratypen (TMP).

Eine weitere Art mit hellgesäumten Seiten der Flügeldecken, die sich von den anderen durch die Form der Maxillarpalpen deren letztes Glied an der Spitze stark verbreitert und dann stark eingeschnürt ist, die Form der Fühler, der Terminalia und des Kopulationsapparates unterscheidet.

9. *Sphinginopalpus (Sphinginafricanus) tergalis* sp. nov.

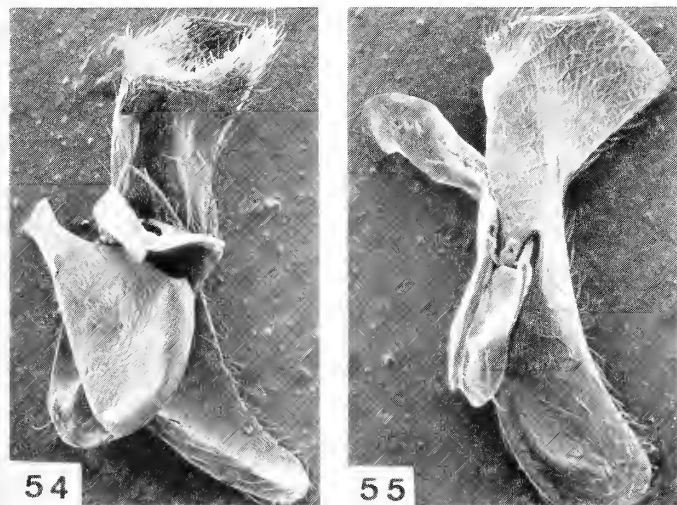


Abb. 54-55. *Sphinginopalpus (Sphinginafricanus) tergalis* sp. nov. ♂: 54-55, Maxillarpalpen (x150) (54, von oben; 55, von unten).

schwarz, nur die Tarsen gelb, 4 vordere Tibien kaum aufgehell.

Kopf mit den Augen ein wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 54- 55. Fühler (Abb. 56) fast so lang wie die Flügeldecken, Glied 3 so lang wie 4. Halsschild länger als breit (18x17), also verhältnismässig kurz; Seiten auf dem vorderen Teil stark gerundet, dann zur Basis ziemlich stark verengt; Oberfläche auf dem basalen Teil etwas stärker chagriniert als vorne. Flügeldecken oval; falsche Epipleuren ca. 70% der Länge

MÄNNCHEN (Abb. 54-59).

Länge 2,5 mm.

Kopf schwarz, von der Mitte der Augen nach vorne, einschliesslich der Wangen, gelb, über jeder Fühlerwurzel ein kleiner brauner Flecken; Maxillarpalpen schwarz, nur Glied 1 leicht aufgehell; Fühlerglieder 1 und 2 gelb, 3 und folgende gebräunt, 3 bis 5 oder 6 auf der Unterseite aufgehell, folgende mehr oder weniger gebräunt; Halsschild schwarz, ungefähr die basale Hälfte des abgeflachten Teils gelbbraun; Schildchen, Flügeldecken und Unterseite schwarz; Beine

einnehmend, kaum merklich krenuliert, sonst wie bei *curvipalpis*; geflügelt. Tergit 8 (Abb. 57) auffällig lang und tief ausgeschnitten und ausserdem mit 2 langen, schmalen, spitz zulaufenden Fortsätzen versehen. Sternit 8 Abb. 58.

Kopulationsapparat Abb. 59 dorsal.

Holotypus (TMP), 1 Paratypus (NHMB): South Africa, Natal: Weza, Bangeni forest, sifted forest litter, 30°38'S, 29°39'E, 21.xi.1989, E-Y:2706, S. Endrödy-Younga, I. Klimaszewski.

Die neue Art ist auffällig durch ihren verhältnismässig kurzen Halsschild, der fast so breit wie lang ist und das Tergit 8 mit den beiden langen, schmalen Fortsätzen in der Mitte.

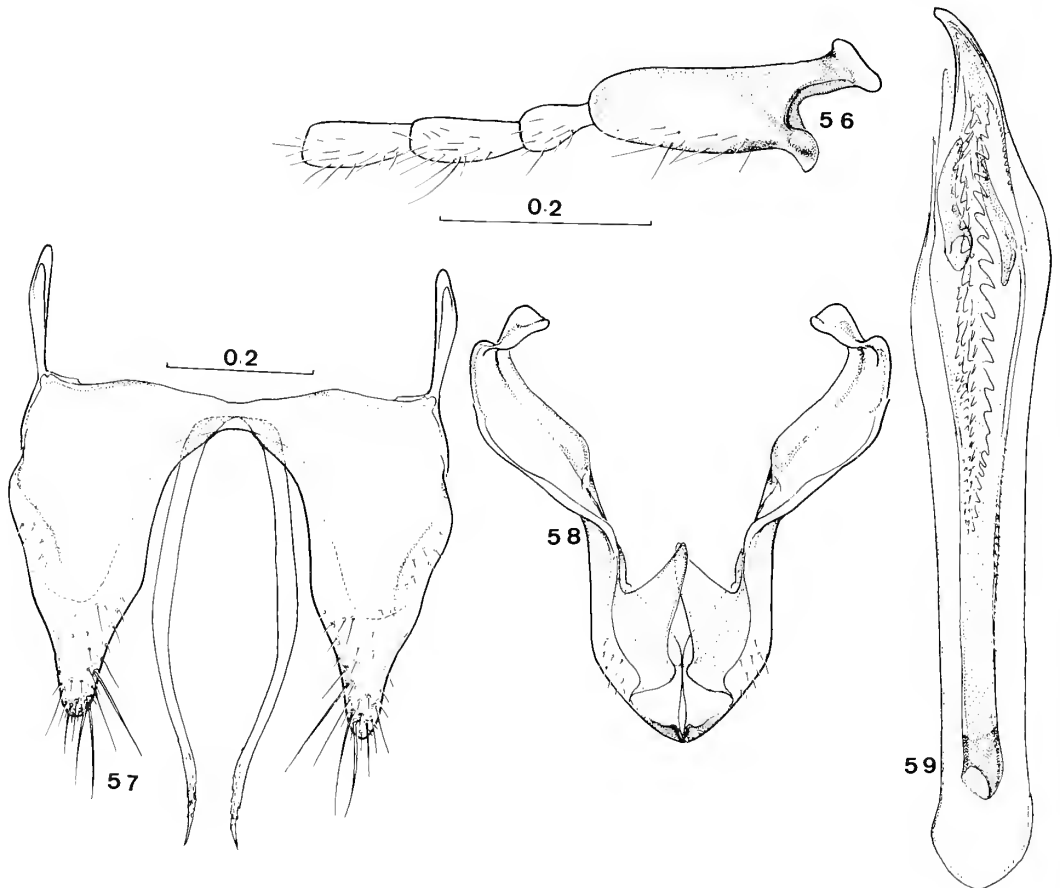


Abb. 56-59. *Spbinginopalpus (Spbinginafricanus) tergalis* sp. nov. ♂: 56, Fühlerglieder 1-4; 57, Tergit 8; 58, Sternit 8; 59, Kopulationsapparat (dorsal). Massstab von 56 auch für 58, 59.

10. *Sphinginopalpus (Sphinginafricanus) bimaculiceps* sp. nov.

MÄNNCHEN (Abb. 60-68).

Länge 2,5 - 2,7 mm.

Kopf schwarz, neben jedem Auge ein kleiner gelber Flecken, der oft bis zur Fühlerwurzel reicht; Maxillarpalpen vorwiegend schwarz, teils kaum aufgehell; Fühler vorwiegend gelb, Glied 1 auf der Oberseite schwarz, letzte 1 bis 4 Glieder manchmal mehr oder weniger angedunkelt; Halsschild schwarz, Basis gelb bis bräunlich; Schildchen und Flügeldecken schwarz, Tibien seltener aufgehell, alle Tarsen gelb, nur bei 1 Exemplar sind die hinteren Tarsen angedunkelt.

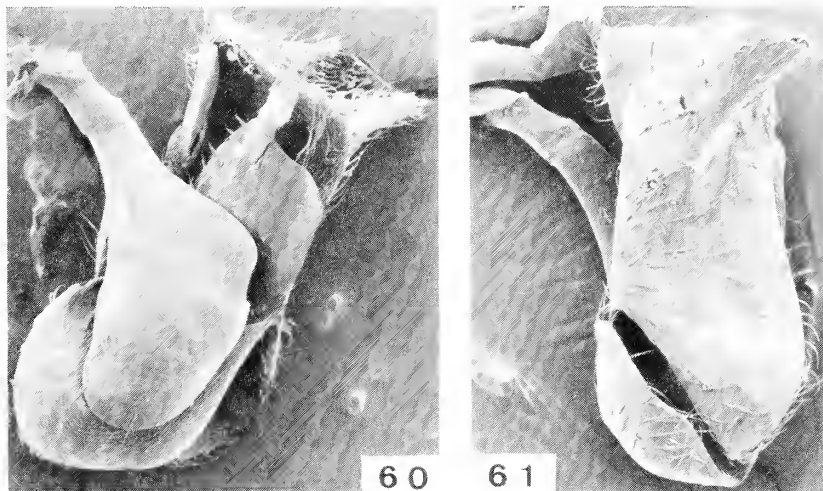


Abb. 60-61. *Sphinginopalpus (Sphinginafricanus) bimaculiceps* sp. nov. ♂: 60-61, Maxillarpalpen (x155) (60, von oben; 61, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert bis fast glatt. Maxillarpalpen (Abb. 60-61). Fühler (Abb. 62) ungefähr so lang wie die Flügeldecken, Glied 1 mit einem spitzwinkligen Zahn vor der Basis, übrige fast parallel. Halsschild länger als breit (21x18), sonst wie *curvipalpis* jedoch etwas weniger tief und weniger dicht punktiert. Tergit 8 Abb. 63. Sternit 8 Abb. 64, Spiculum Abb. 65. Tegmen Abb. 66.

Kopulationsapparat Abb. 67 dorsal, Abb. 68 Profil.

WEIBCHEN.

Kopf einfarbig schwarz, Fühler gelb, nur die Spitze von Glied 11 kurz dunkel, sonst wie das ♂ gefärbt. Schulterbeulen nur angedeutet, wahrscheinlich ungeflügelt.

Holotypus (TMP): South Africa, E Transvaal: Graskop, xii.1974, P. E. Reavell; Nelshoogte, Devils Knuckle, grassnetting, 4.xii.1986, 25°47'S, 30°49'E, E-Y:2350, S. Endrödy-Younga, 1 Paratypus (TMP); Bothasnek, 1450 m, 23.xi.1987, W. Wittmer, 2 Paratypen (NHMB); Mac-Mac 10 km N of

Sabie, 17.i.1989, 25°02'S, 30°48'E, E. Grobbelaar, 2 Paratypen (NCI), 2 Paratypen (NHMB); Berlin Gorge- edge, beating bushes, grassnetting, 25°32'S, 30°44'E, 8.xii.1986, 3.-4.ii.1987, E-Y:2365, 2405, 2413, S. Endrödy-Younga, 3 Paratypen (TMP), 1 Paratypus (AMG); Nelspruit Nat. Res. rivulet vall. 25°29'S, 30°55'E, 5.xii.1986, E-Y:2355, S. Endrödy-Younga, 1 Paratypus (TMP).

Die neue Art ist neben *isidengensis* Wittmer zu stellen, von der sie sich durch das verschieden gebaute Fühlerglied 1, die Terminalia und den Kopulationsapparat unterscheidet.

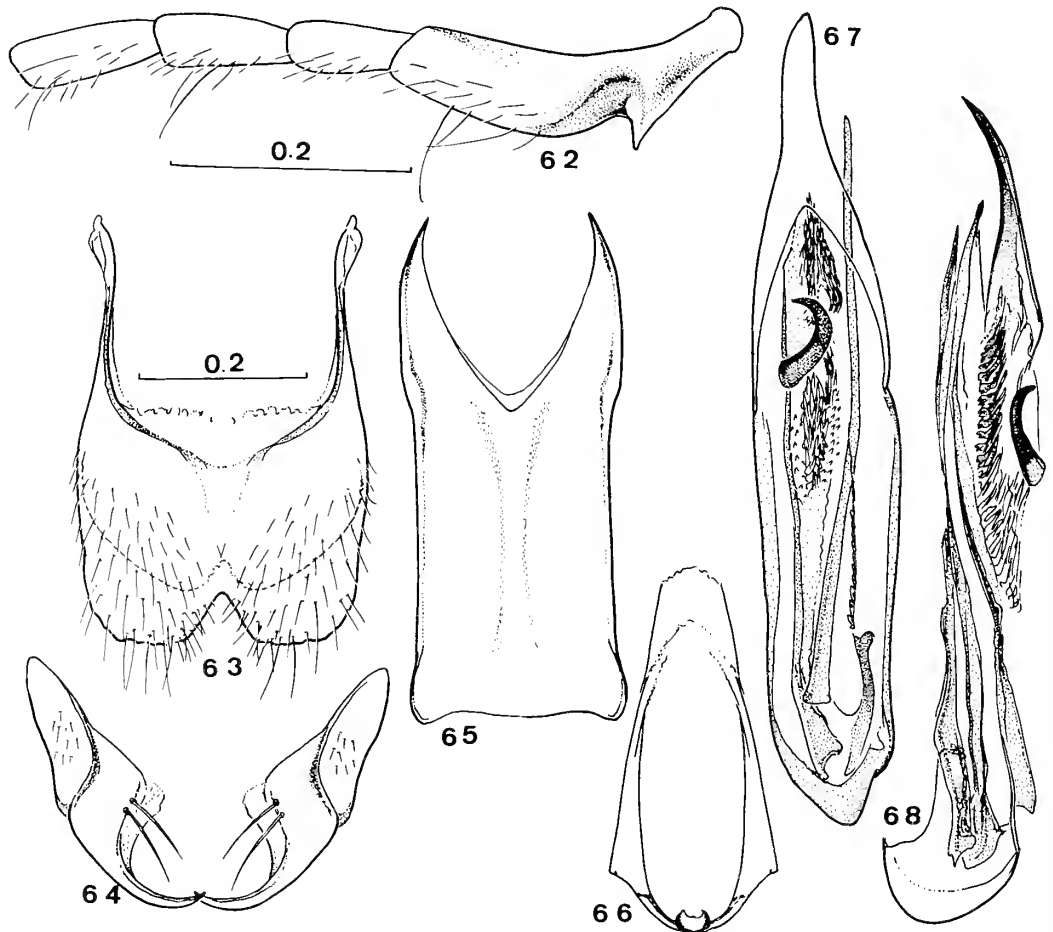


Abb. 62-68. *Sphinginopalpus (Sphinginafricanus) bimaculiceps* sp. nov. ♂: 62, Fühlerglieder 1-4; 63, Tergit 8; 64, Sternit 8; 65, Spiculum; 66, Tegmen; 67-68, Kopulationsapparat (67, dorsal; 68, Profil). Massstab von 63 auch für 64-68.

11. *Sphinginopalpus (Sphinginafricanus) isidengensis* sp. nov.

MÄNNCHEN (Abb. 69-74).

Länge 2,2- 2,3 mm.

Kopf schwarz, von der Mitte der Augen nach vorne, inklusive der Wangen, gelb; Maxillarpalpen schwarz; Fühler gelb, letzte 1 bis 2 Glieder manchmal angedunkelt, 1 mit einem länglichen, schwarzen Flecken gegen die Spitze auf der Oberseite; Halsschild schwarz, abgeflachter basaler Teil orange; Schildchen, Flügeldecken und Unterseite schwarz; Hinterbeine schwarz, Hintertarsen gelb, 4



Abb. 69-70. *Sphinginopalpus (Sphinginafricanus) isidengensis* sp. nov. ♂: 69-70, Maxillarpalpen (x150) (69, von oben; 70, von unten).

Vorderschenkel schwarz, an den Knien mehr oder weniger aufgeheilt, 4 Vordertibien dunkel, bis zur Hälfte oder darüber hinaus gelb, 4 Vordertarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 69-70. Fühler (Abb. 71) nur wenig kürzer als die Flügeldecken, Glied 3 so lang wie 4. Halsschild länger als breit (19x14), sonst wie bei *curvipalpis*. Flügeldecken oval, falsche Epipleuren ca. 80% der Länge einnehmend, schwach krenuliert; sonst wie bei *curvipalpis*. Tergit 8 Abb. 72. Sternit 8 Abb. 73.

Kopulationsapparat Abb. 74 dorsal.

WEIBCHEN.

Fühlerglied 1 ohne schwarzen Flecken, sonst wie das ♂ gefärbt. Fühlerglied 1 lang und schmal, ohne Zahn. Flügeldecken mit kleiner, spitzer Schulterbeule, welche nach hinten ein wenig als stumpfer Kiel verlängert ist (stärker ausgeprägt als beim ♂), ungeflügelt.

Holotypus ♂ und 2 Paratypen (TMP): South Africa, Cape Prov.: Amatole, Isidenge Forest Station, grass tussocks and grassnetting Arum fl., 32°41'S, 27°15'E, 18.xi.1987, E-Y:2524, S. Endrödy-Younga.

Die neue Art ist neben *recurvus* Wittmer zu stellen, vergleiche Abbildungen der Terminalia und des Kopulationsapparates.

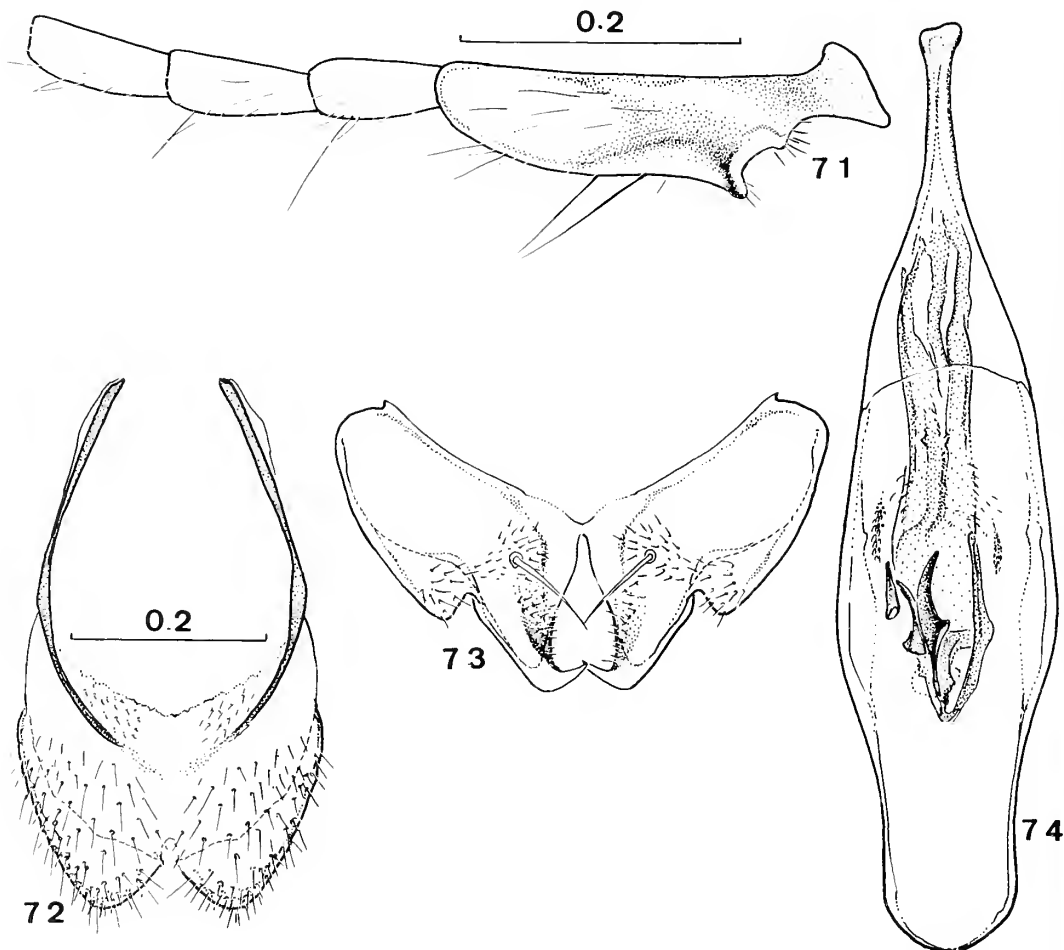


Abb. 71-74. *Sphinginopalpus (Sphinginafricanus) isidengensis* sp. nov. ♂: 71, Fühlerglieder 1-4; 72, Tergit 8; 73, Sternit 8; 74, Kopulationsapparat (dorsal). Massstab von 72 auch für 73, 74.

12. *Sphinginopalpus (Sphinginafricanus) martini* Pic

Sphinginopalpus martini Pic, 1904: 12.

MÄNNCHEN (Abb. 75-83).

Im MP werden 2 Syntypen ♂ ♀ dieser Art aufbewahrt, die ich als Lectotypus und Paralectotypus bezeichne, Fundort: Natal, Dr. Martin. Für die Abbildungen diente der Lectotypus mit Ausnahme von Abb. 75, für die 1 Exemplar von De Rust verwendet wurde. Maxillarpalpen Abb. 75-77. Fühler Abb. 78. Tergit 8 Abb. 79. Sternite 7 und 8 Abb. 80- 81. Kopulationsapparat Abb. 82 dorsal.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

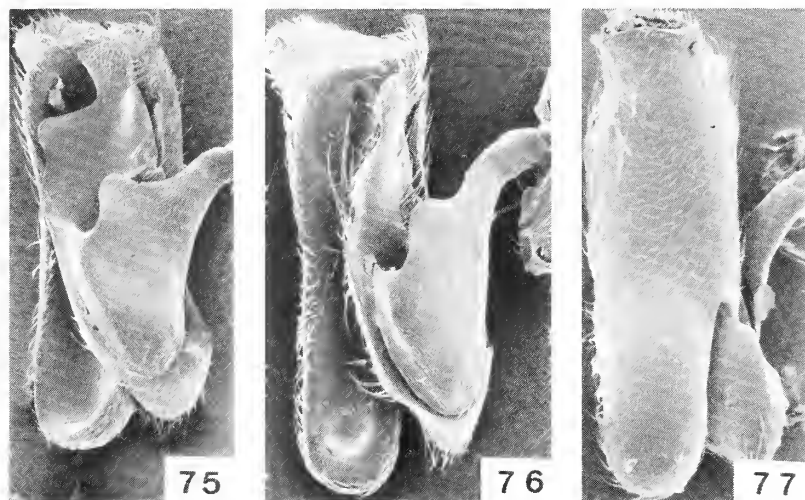


Abb. 75-77. *Sphinginopalpus (Sphinginafricanus) martini* Pic ♂: 75-77, Maxillarpalpen (x130)
(75, von oben, 76, von oben in anderem Winkel; 77, von unten)

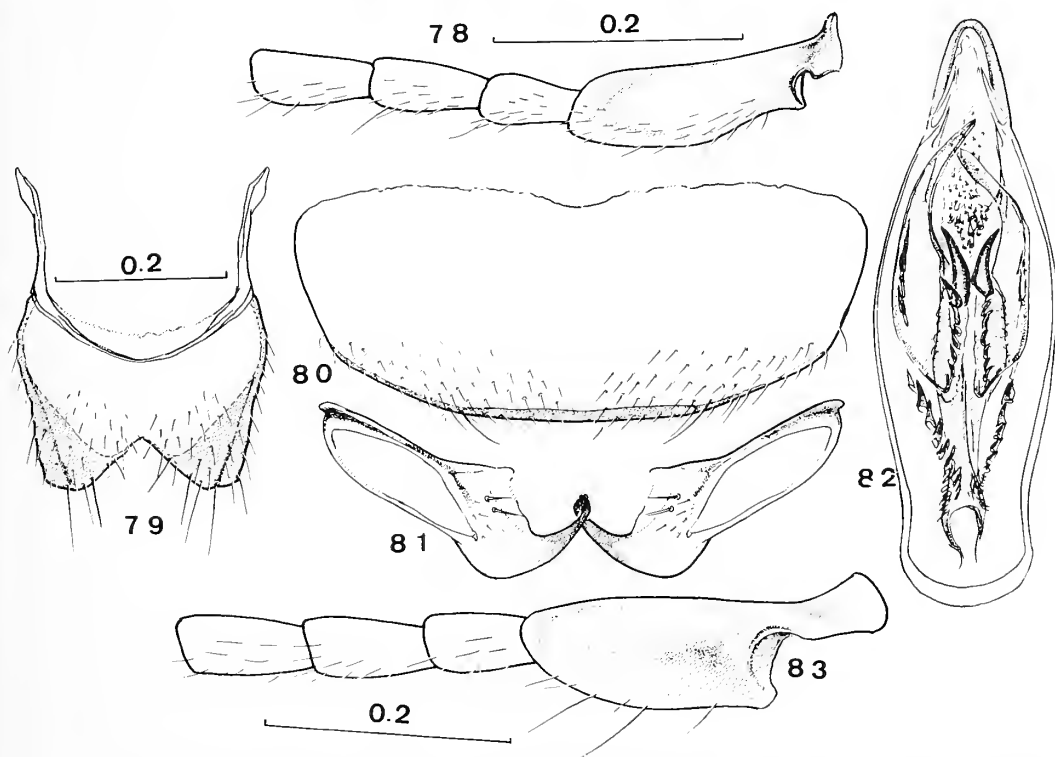


Abb. 78-83. *Sphinginopalpus (Sphinginafricanus) martini* Pic ♂: 78, Fühlerglieder 1-4; 79, Tergit 8; 80, Sternit 7; 81, Sternit 8; 82, Kopulationsapparat (dorsal); 83, Fühlerglieder 1-4. Massstab von 78 auch für 80-83. Die Abbildungen 75 und 83 von De Rust Valley, die übrigen vom Lectotypus.

UNTERSUCHTES MATERIAL: Natal: Weza, Impetyene grassveld, flowering grass, 30°37'S, 29°42'E, 21-25.xi.1989, E-Y:2680, 2712, 2717, S. Endrödy-Younga, I. Klimaszewski, 2 Ex. (TMP), 2 Ex. (NHMB); Karkloof Falls Nature Reserve, 22 km N Pietermaritzburg, 6.x.1986, W. Wittmer (NHMB); St Lucia, 10 m, 25-27.x.1981, J. & S. Klapperich, 54 Ex. (NHMB), bei weiteren 12 Ex. mit Fundort: Cape Prov., De Rust (Valley), 29.xi.1981, J. & S. Klapperich, muss angenommen werden, dass derselbe unrichtig ist und die Tiere ebenfalls aus St Lucia stammen.

Die Form von Fühlerglied 1 weicht bei dem ganzen Material von dem des Lectotypus (Abb. 83) ab, da jedoch der Kopulationsapparat und die Terminalia keine Unterschiede zeigen, stelle ich das Material zu *martini*.

13. *Sphinginopalpus (Sphinginafricanus) consimilis* sp. nov.

MÄNNCHEN (Abb. 84-85).

Länge 2,3 mm.

Diese Art ist äusserlich und auch aufgrund der Terminalia nicht von *martini* zu unterscheiden. Der Kopulationsapparat (Abb. 85) ist jedoch sehr verschieden gebaut und besteht somit kein Zweifel, dass *consimilis* einer anderen Art angehört. Fühler (Abb. 84) ähnlich wie bei *martini*.

Holotypus (NHMB): Natal: Nkandla Forest, 6.i.1982, P. E. Reavell.

Diese neue Art ist neben *martini* Pic zu stellen.

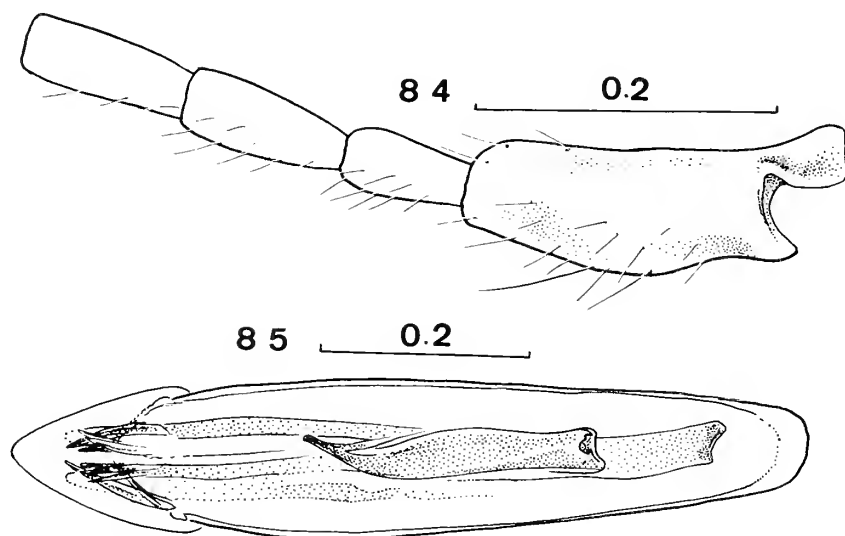


Abb. 84-85. *Sphinginopalpus (Sphinginafricanus) consimilis* sp. nov. ♂: 84, Fühlerglieder 1-4; 85, Kopulationsapparat (dorsal).

14. *Sphinginopalpus (Sphinginafricanus) formicarius* (Gorham)

Chalichorus formicarius Gorham, 1901: 358. *Sphinginopalpus formicarius* Gorham - Champion, 1922: 330, T. 5, f. 22.

MÄNNCHEN (Abb. 86-93).

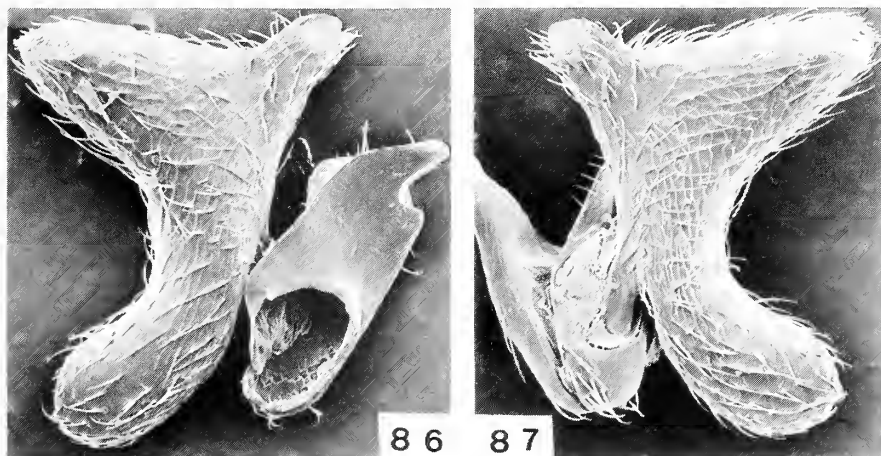


Abb. 86-87. *Sphinginopalpus (Sphinginafricanus) formicarius* (Gorham) ♂: 86-87, Maxillarpalpen (x185) (86, zeigt links Glied 3 von unten, daneben Glied 2 von innen; 87, von unten).

Im BM wird der Holotypus, neu als Lectotypus bezeichnet, aufbewahrt, der von Malvern, Natal, stammt. Vom gleichen Fundort und gleichen Datum (vi.1897) befindet sich auch 1 ♂ im BM, dessen Maxillarpalpen von Champion abgebildet werden. Zwei weitere ♀ von Malvern sind im MP als Typen bezeichnet und jetzt von mir mit Paralectotypen-Etiketten versehen worden.

UNTERSUCHTES MATERIAL: Natal: Durban. F. Muir, 2 ♂ (BM); St Lucia, 10 m, 25.-27.x.1981, J. & S. Klapperich, 22 Ex. (NHMB); Eshowe, Glinza Forest, 19.xii.1985, P. E. Reavell, 12 Ex. (NHMB); Transkei: Dwesa coast, coastal grassland, 32°17'S, 28°51'E, 16.xii.1979, 28.ii.1985, E-Y:1687, 2175, S. Endrödy-Younga, 6 Ex. (TMP), 3 Ex. (NHMB).

MÄNNCHEN.

Länge 2 - 2,1 mm.

Kopf schwarz, von der Mitte der Augen nach vorne, einschliesslich der Wangen, gelb; Maxillarpalpen schwarz; Fühler schwarz, Glieder 1 und 2 gelb, 1 mit einem Längsflecken auf der Oberseite gegen die Spitze, 2 meistens mehr oder weniger angedunkelt auf der Oberseite; Halsschild schwarz, abgeflachter Teil an der Basis gelblich; Schildchen, Flügeldecken und Beine schwarz, mit Ausnahme der Basis der Schenkel und der Spitzen der Tibien bei den Mittel- und Vorderbeinen, die gelblich sind, alle Tarsen gelb, die hinteren oft stark angedunkelt.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche feinstens chagriniert, fast glatt, Maxillarpalpen Abb. 86-87. Fühler (Abb. 88) ungefähr so lang wie die Flügeldecken, Spitze von Glied 1 ein wenig über die Basis von 2 reichend, 3 so lang wie 4. Halsschild länger als breit (18x13), vor der Mitte am breitesten, dann nach hinten zuerst leicht gerundet, dann fast gerade verschmälert; Seitenrand vor der Basis erlöschend, Basalrand nur angedeutet; Scheibe auf den vorderen 2/3 stark aufgewölbt, basaler Teil abgeflacht; ganze Oberfläche chagriniert. Flügeldecken oval, ungefähr in der Mitte am breitesten; Schulterbeulen deutlich vorstehend; Punkte ziemlich tief in Reihen angeordnet, erst kurz vor der Spitze erlöschend; falsche Epipleuren ca. 70% der Länge einnehmend, auf dem vorderen Teil krenuliert; ziemlich zahlreiche, lange, aufstehende Haare vorhanden; geflügelt. Hinterschienen gegen die Spitze allmählich schwach verbreitert. Tergit 8 Abb. 89. Sternit 8 Abb. 90. Spiculum Abb. 91.

Kopulationsapparat Abb. 92 dorsal, Abb. 93 Profil.

WEIBCHEN.

Wie das ♂ gefärbt, mit Ausnahme des schwarzen Kopfes und der Fühler, die heller sind, dunkle

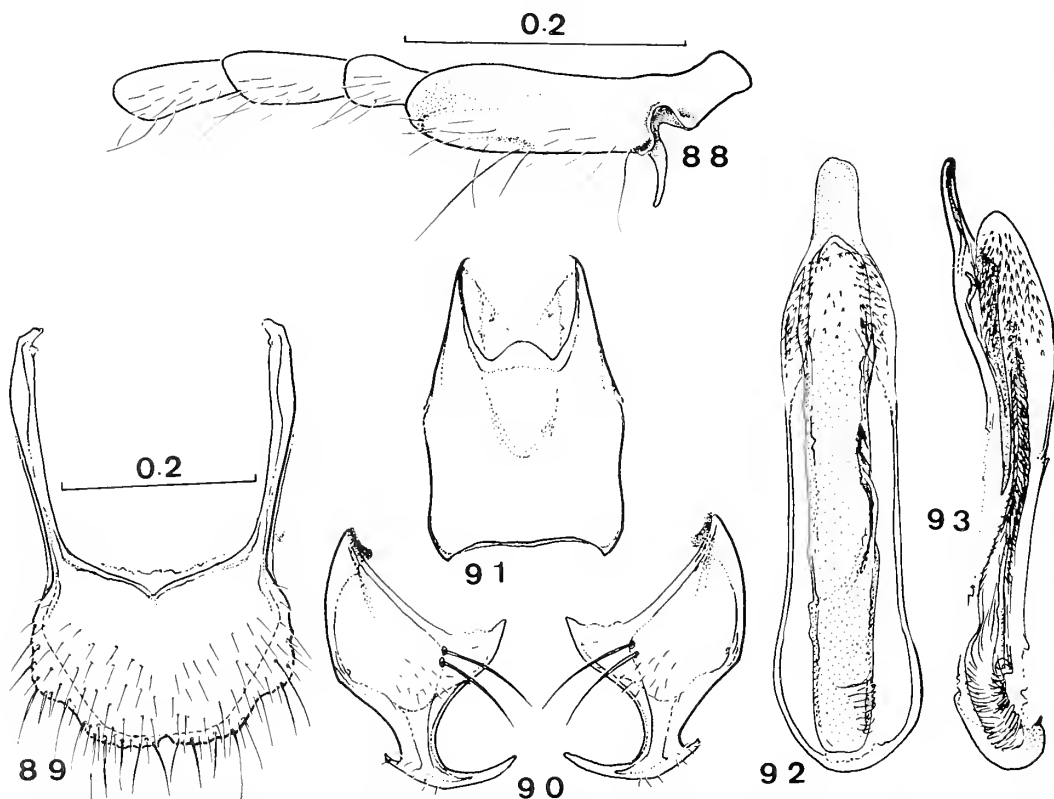


Abb. 88-93. *Sphingopalpus (Sphinginafricanus) formicarius* (Gorham) ♂: 88, Fühlerglieder 1-4; 89, Tergit 8; 90, Sternit 8; 91, Spiculum; 92-93, Kopulationsapparat (92, dorsal; 93, Profil). Massstab von 89 auch für 90-93.

Färbung auf Glied 1 fehlt oft, oder ist höchstens ungedeutet, 2 und 3 oder auch weitere Glieder hell. Fühlerglied 1 sehr lang und schmal, ohne Zahn. Flügeldecken mit kleiner spitzer Schulterbeule; ungeflügelt.

15. *Sphinginopalpus (Sphinginafricanus) recurvus* sp. nov.

MÄNNCHEN (Abb. I, K, 94-100).

Länge 2,5 mm.



Kopf schwarz, Vorderkopf ungefähr von der Mitte der Augen an gelb; Maxillarpalpen hellbraun, wenige Stellen angedunkelt; Fühler schwarz, Glieder 1 und 2 gelb, auf der Oberseite angedeutet dunkel, oder nur 1 auf der Oberseite gegen die Spitze mit einem kurzen schwarzen Wisch, 3 bis 5 auf der Unterseite aufgehellt; Halsschild schwarz, Basis gelbbraun; Schildchen und Flügeldecken schwarz; Schenkel schwarz, die 4 vorderen in variablem Umfang gelb, Hinterschienen schwarz, die 4 vorderen z. T. fast vollständig hell, alle Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 94. Fühler (Abb. 95) ungefähr so lang wie die Flügeldecken, Zahn auf Glied 1 wenig lang, einen schwachen spitzen Winkel bildend. Halsschild länger als breit (21x17), sonst wie *curvipalpis*, Oberfläche fein chagriniert, ohne glatte Stellen, feinste Rippen nur angedeutet. Flügeldecken wie *curvipalpis*, falsche Epipleuren deutlicher krenuliert. Tergit 8 (Abb. 96) wenig tief, breit ausgerandet. Sternit 8 (Abb. 98) jederseits mit einem kräftigen, nach innen gekrümmten Haken, Sternit 7 (Abb. 97) mit leicht gewelltem Apikalrand. Gesamtansicht Abb. I, K.

Kopulationsapparat Abb. 99 dorsal, Abb. 100 Profil.

Abb. 94. *Sphinginopalpus (Sphinginafricanus) recurvus* sp. nov. ♂: 94, Maxillarpalpus (x130) (von oben).

WEIBCHEN (Abb. A-C, G).

Kopfeinfarbig schwarz, sonst wie das ♂ gefärbt. Übrige Beschreibung mit *repandus* übereinstimmend. Gesamtansicht Abb. A, B. Maxillarpalpen Abb. C. Basis des Halsschildes Abb. G.

Holotypus und 42 Paratypen (TMP), 17 Paratypen (NHMB), 4 Paratypen (AMG): South Africa, SW Natal: Weza, indigenous forest, 30°35'S, 29°45'E, grassnetting, 24.xii.1985, E-Y:2160, S. Endrödy-Younga.

Die Maxillarpalpen erinnern etwas an *emarginatus* Wittmer, neben welchen die neue Art zu stellen ist, doch ist das Fühlerglied 1, die Terminalia und der Kopulationsapparat verschieden gebaut.

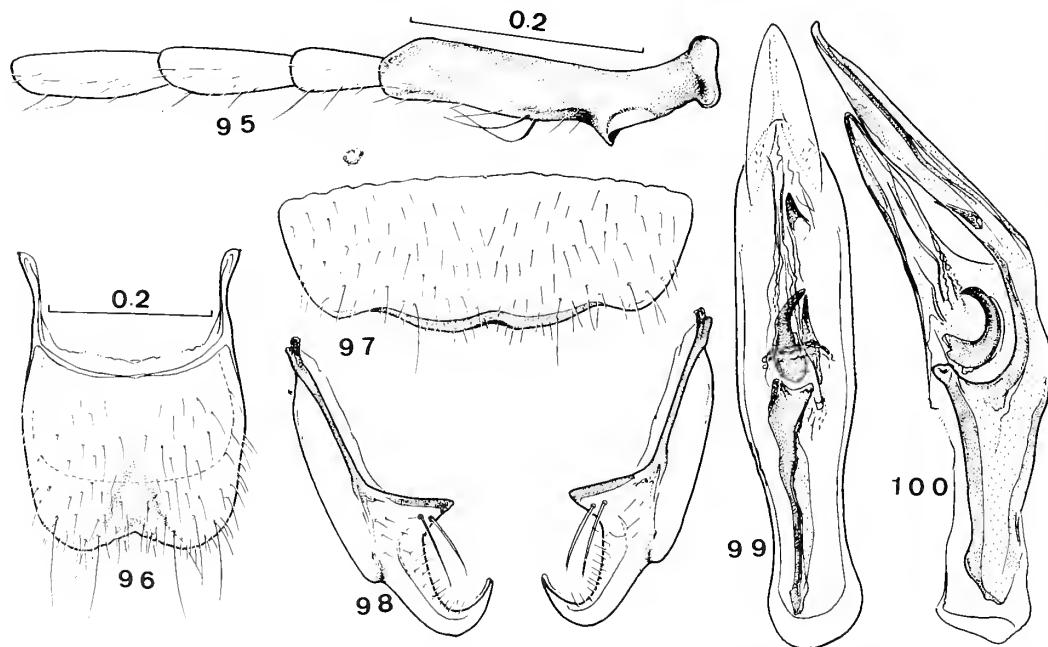
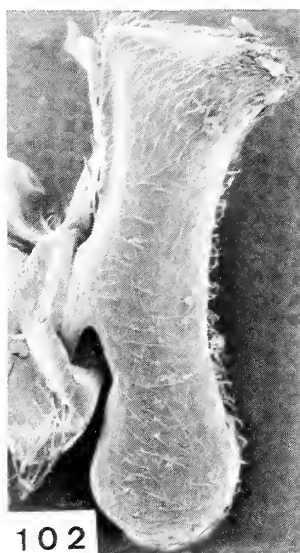


Abb. 95-100. *Sphinginopalpus (Sphinginafricanus) recurvus* sp. nov. ♂: 95, Fühlerglieder 1-4; 96, Tergit 8; 97, Sternit 7; 98, Sternit 8; 99-100, Kopulationsapparat (99, dorsal; 100, Profil). Massstab von 96 auch für 97 und 98 auch für 99, 100.

16. *Sphinginopalpus (Sphinginafricanus) recurvus planicornis* ssp. nov.



MÄNNCHEN (Abb. 101-103).

Länge 2,5 mm.

Diese Rasse ist weit verbreitet und unterscheidet sich von der Nominatform hauptsächlich durch den Bau der Fühler (Abb. 103), Glied 1 ist weniger schlank, nach dem etwas kräftigeren Zahn schwach bauchig verdickt, 3 bis 5 sind deutlich abgeflacht und ein wenig breiter als die folgenden, auch 6 zeigt noch eine leichte Verbreiterung. Die Färbung der Fühler ist durchwegs dunkler, bereits ab Glied 3 schwarz, 2 oft mit einem kleinen verschwommenen Flecken auf der Oberseite, ebenso 1, oder 1 und 2 sind einfarbig gelb. Die Maxillarpalpen (Abb. 101-102) haben grosse

Abb. 101-102. *Sphinginopalpus (Sphinginafricanus) recurvus planicornis* ssp. nov. ♂: 101-102, Maxillarpalpen (x130) (101, von oben; 102, von unten).

Ähnlichkeit mit der Nominatform, vergleiche Abbildungen, sie sind jedoch etwas länger und breiter. Die Terminalia weichen im Bau nur geringfügig ab. Ich möchte nicht entscheiden, ob es sich um eine Rasse, oder um eine eigene Art handelt, letzteres scheint mit eher wahrscheinlich.

Holotypus und 10 Paratypen (TMP), 6 Paratypen (NHMB), 1 Paratypus (AMG): South Africa, Natal: Karkloof forest and grassveld, 29°19'S, 30°15'E, 2.-7.xii.1989, E-Y:2729, 2737, 2748, 2749, 2758, S. Endrödy-Younga, I. Klimaszewski; Doreen Clark Nature Reserve, sifted forest litter, 29°34'S, 30°17'E, 8.xii.1989, E-Y:2750, S. Endrödy-Younga, I. Klimaszewski, 1 ♂ Paratypus (TMP); Pietermaritzburg, Town Bush Forest, 29°36'S, 30°23'E, 27.ii.1984, C. G. E. Moolman, 16 Paratypen (NCI), 4 Paratypen (NHMB), 2 Paratypen (AMG); Karkloof Falls near Howick, 29°25'S, 30°17'E, 26.xi.1984, R. Oberprieler, C. G. E. Moolman, 6 Paratypen (NCI).

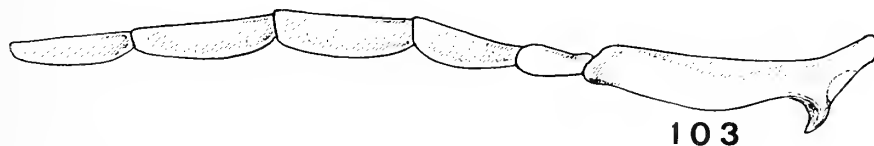


Abb. 103. *Sphinginopalpus (Sphinginafricanus) recurvus planicornis* ssp. nov. ♂:103, Fühlerglieder 1-6.

17. *Sphinginopalpus (Sphinginafricanus) repandus* sp. nov.

MÄNNCHEN (Abb. 104-109).

Länge 2,5 mm.



Abb. 104-105. *Sphinginopalpus (Sphinginafricanus) repandus* sp. nov. ♂: 104-105, Maxillarpalpen (x130) (104, von oben; 105, von unten).

Kopf schwarz, Vorderkopf ungefähr von der Mitte der Augen an, gelb; Maxillarpalpen schwarz, teils gelb, seltener zum grössten Teil gelb; Fühler gelb, manchmal sind die letzten Glieder schwach andunkelt; Halsschild schwarz, Basis ziemlich breit gelb bis orange; Schildchen und Flügeldecken schwarz; 4 Vorderbeine gelb, Hintertibien schwarz, Hinterschenkel oft teils gelb (Basis), Hintertarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stime leicht gewölbt;

Oberfläche glatt. Maxillarpalpen Abb. 104-105. Fühler (Abb. 106) nur wenig länger als die Flügeldecken, fast parallel. Halsschild länger als breit (19x15), vorderer Teil stark aufgewölbt, Basis breit abgeflacht; Seiten fast bis zur Mitte leicht gerundet, dann schwach verengt; Rand an der Basis breiter als die Seiten, kurz vor der Basis erloschen; Oberfläche fein chagriniert, auf der Mitte der Scheibe fast glatt, gegen die Seiten oft mit 2 feinen Rippen. Flügeldecken länglichoval, Schultern normal entwickelt; falsche Epipleuren lang, scharf, feinstens krenuliert; Oberfläche glatt, Punkte ziemlich grob, besonders an der Basis teils in Reihen angeordnet, Punkte gegen die Spitze fast ganz erloschen; einzelne lange, abstehende Haare vorhanden; geflügelt. Tergit 8 (Abb. 107) apikal schräg abgestutzt, an der Spitze kurz ausgerandet. Sternit 8 Abb. 108.

Kopulationsapparat (Abb. 109) dorsal, neben dem Innensack sind 3 kleine, stark sklerotisierte Hörnchen sichtbar.

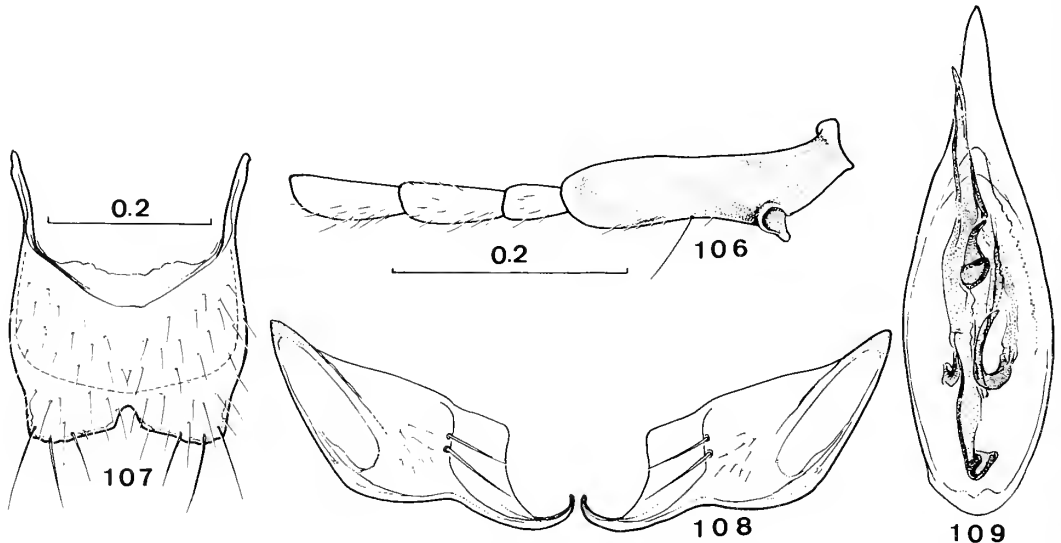


Abb. 106-109. *Sphinginopalpus (Sphinginafricanus) repandus* sp. nov. ♂: 106, Fühlerglieder 1-4; 107, Tergit 8; 108, Sternit 8; 109, Kopulationsapparat (dorsal). Massstab von 106 auch für 108 und 107 auch für 109.

WEIBCHEN.

Kopf einfarbig schwarz, sonst wie das ♂ gefärbt. Letztes Glied der Maxillarpalpen zur Spitze schwach verbreitert. Fühlerglied 1 einfach, schmal und lang, fast 4 mal länger als 2. Flügeldecken breiter als beim ♂, Schulterbeulen ein wenig reduziert; ungeflügelt.

Holotypus und 1 Paratypus ♂ (NHMB): South Africa, Transvaal: Bothasnek, 1450 m, 23.xi.1987, W. Wittmer. Natal: Cathedral Peak, Drakensberg, 6.xi.1981, J. & S. Klapperich, 4 Paratypen (NHMB); idem Mike's Pass, 1700 m, 28°48'S, 29°14'E, 24.ii.1984, C. G. E. Moolman, 5 Paratypen (NCI); 2 Paratypen (NHMB); idem area above Mike's Pass, 1973 m, 28°59'S 29°14'E, 19.-23.ii.1973, B. Grobbelaar, 2 Paratypen (NCI); idem Arensig Mt., 20.xii.1986, P. Reavell, 1 Paratypus (NHMB); idem Mt. Nhlosane near Dargle, 1600 m, 29°33'S, 29°58'E, C. G. E. Moolman, 10 Paratypen (NCI), 2 Paratypen (AMG); Nelshoogte Forest Station, Knuckles grassveld, 1.-4.xii.1986, 25°47'S,

30°49'50"E, E-Y:2339, 2350, S. Endrödy-Younga, 2 Paratypen (TMP), 1 Paratypus (NHMB).

Diese neue Art ist nahe mit *obtusodentatus* Wittmer verwandt. Sie unterscheidet sich durch die verschieden gebauten Maxillarpalpen, Fühler und Terminalia.

18. *Sphinginopalpus (Sphinginafricanus) emarginatus* sp. nov.

MÄNNCHEN (Abb. 110-115).

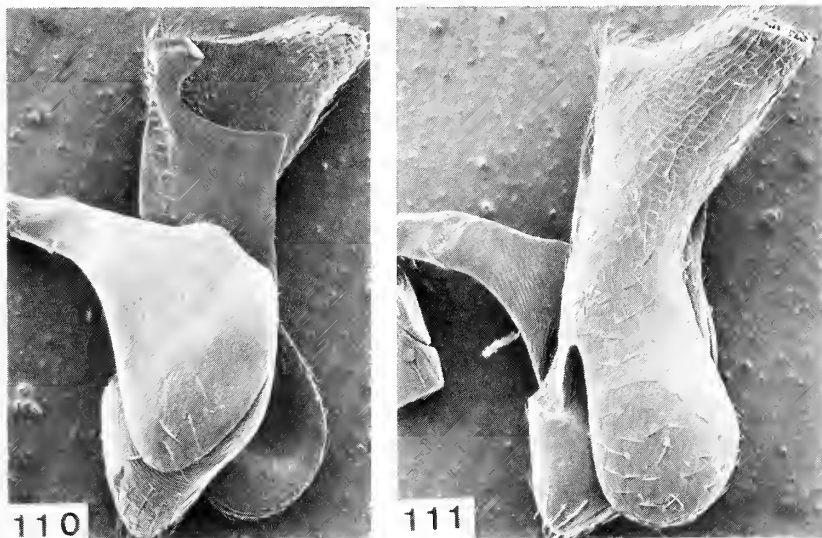


Abb. 110-111. *Sphinginopalpus (Sphinginafricanus) emarginatus* sp. nov. ♂: 110-111, Maxillarpalpen (x150) (110, von oben; 111, von unten).

Länge 2,2-2,4 mm.

Kopf schwarz, Vorderkopf von ungefähr der Mitte der Augen, inklusive der Wangen, gelblich; Maxillarpalpen schwarzbraun, teils aufgeheilt; Fühler dunkel, Glieder 1 und 2 gelb, 3 und 5 aufgeheilt, oben s c h w a c h angedunkelt, 1 mit einer kleinen dunkeln Stelle an der Spitze auf der O b e r s e i t e ; H a l s s c h i l d

schwarz, Basis fast auf der ganzen abgeflachten Stelle gelb; Schildchen und Flügeldecken schwarz; Beine schwärzlich, Vorderschenkel innen aufgeheilt, die übrigen an der Basis kurz gelb, 4 Vordertarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 110-111. Fühler (Abb. 112), das Glied 3 so lang wie 4, auf der Zeichnung ist 4 etwas zu lang. Halsschild länger als breit (22x15), vorderer Teil stark aufgewölbt, Basis breit abgeflacht; Seiten bis zur Mitte gerundet, dann verengt; Oberfläche auf dem abgeflachten Teil stärker chagriniert als vorne. Flügeldecken länglichoval, Schultern normal entwickelt; falsche Epipleuren lang, scharf, fein krenuliert; Oberfläche glatt, Punkte ziemlich grob, einzelne Punktreihen erkennbar, Punktierung nach hinten schwächer; geflügelt. Tergit 8 (Abb. 113) mit breit aber wenig tief ausgerandeter Spitze. Sternit 8 Abb. 114.

Kopulationsapparat Abb. 115 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz, Fühlerglieder 1 bis 6 einfarbig gelb, sonst wie das ♂ gefärbt.

Flügeldecken breiter als beim ♂, Schulterbeulen angedeutet.

Holotypus and 5 Paratypen (TMP), 2 Paratypen (NHMB): South Africa, Transvaal: Uitsoek Forest Station, beating, 12.ii. und 7.viii.1986, 1100-1200 m, E-Y:2430, 2380, S. Endrödy-Younga; Nelshoogte, riverine forest litter, 1000 m, 2.xii.1986, E-Y:2341, S. Endrödy-Younga, 17 Paratypen (TMP), 7 Paratypen (NHMB), 2 Paratypen (AMG).

Die neue Art ist neben *tubulatus* Wittmer zu stellen und aufgrund der Unterschiede gemäss der Abbildungen leicht zu unterscheiden.

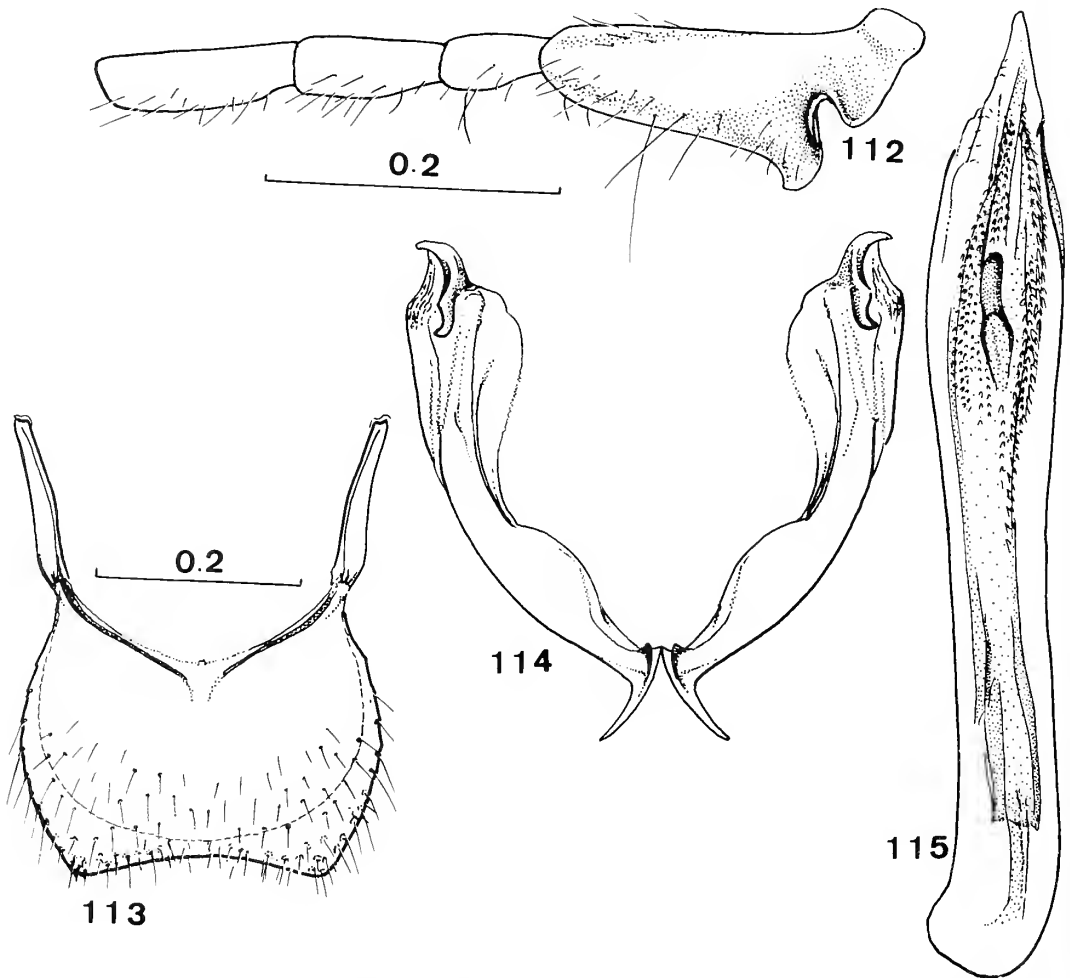


Abb. 112-115. *Sphinginopalpus* (*Sphinginafricanus*) *emarginatus* sp. nov. ♂: 112, Fühlerglieder 1-4; 113, Tergit 8; 114, Sternit 8; 115, Kopulationsapparat (dorsal). Massstab von 112 auch für 114-115.

19. *Sphinginopalpus (Sphinginafricanus) reductosetosus* sp. nov.

MÄNNCHEN (Abb. 116-123).

Länge 2,5 mm.

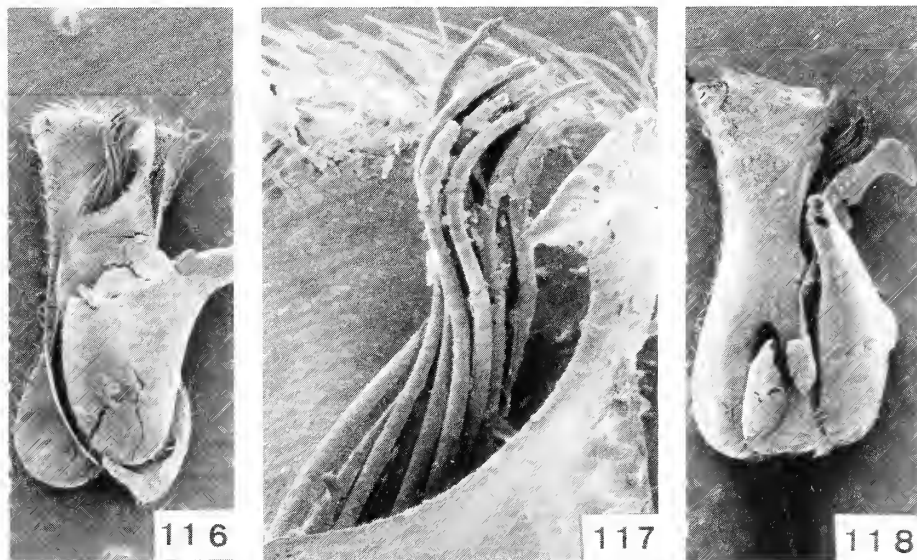


Abb. 116-118. *Sphinginopalpus (Sphinginafricanus) reductosetosus* sp. nov. ♂: 116-118, Maxillarpalpen (116, von oben, x130; 117, Ausschnitt aus der Oberseite, x550; 118, von unten, x130).

Kopf schwarz, von der Mitte nach vorne, inklusive der Wangen, gelb; Fühler schwarz, Glied 1 gelb, an der Spitze auf der Oberseite ein kleiner schwarzer Flecken, 2 bis 4 ganz und Basis von 5 kurz gelb; Halsschild schwarz, Basis ziemlich breit gelb; Schildchen und Flügeldecken schwarz; alle Tarsen gelb, Hinterbeine schwarz, Mittel- und Vorderbeine gelb bis braun, teils leicht angedunkelt.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche feinstens chagriniert, teils fast glatt. Maxillarpalpen Abb. 116-118. Fühler (Abb. 119) so lang wie die Flügeldecken, Glieder 3 bis 10 am Innenrand schwach gerundet, 5 ein wenig verbreitert. Halsschild länger als breit (18x14,5), sonst wie *curvipalpis*; Chagriniierung sehr fein, auf der Scheibe fast glatt. Flügeldecken länglichoval, Schulterbeulen reduziert, leicht spitz vorstehend, sonst wie bei *curvipalpis*, jedoch ungeflügelt und falsche Epipleuren deutlicher. Tergit 8 Abb. 120. Sternit 8 Abb. 121. Spiculum Abb. 122.

Kopulationsapparat Abb. 123 dorsal.

Holotypus und 33 Paratypen (TMP), 18 Paratypen (NHMB), 4 Paratypen (AMG): South Africa, E Transvaal: Berlin, 24°32'S, 30°44'E, gorge edge, beating bushes, 3.ii.1987, E-Y:2405, S. Endrödy-Younga; Nelshoogte, 1000 m, riverine forest litter, 2.xii.1986, E-Y:2341, S. Endrödy-Younga, 1 Paratypus (NHMB).

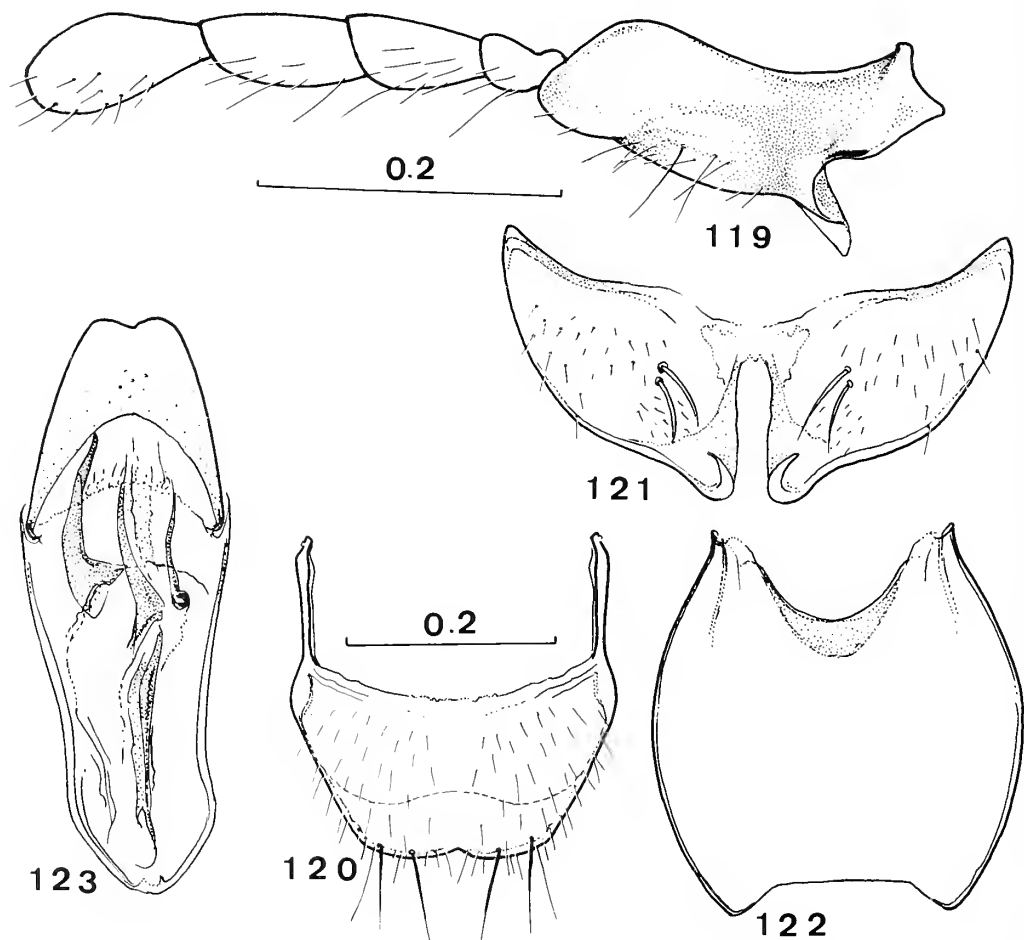


Abb. 119-123. *Sphinginopalpus (Sphinginafricanus) reductosetosus* sp. nov. ♂: 119, Fühlerglieder 1-5; 120, Tergit 8; 121, Sternit 8; 122, Spiculum; 123, Kopulationsapparat (dorsal). Massstab von 119 auch für 121-123.

Der Widerhaken an Glied 2 der Maxillarpalpen ist für diese Art sehr charakteristisch. Aufgrund des verbreiterten Fühlergliedes 5 gehört sie eigentlich zu *bilineaticeps*, *reavelli* und *recurvus planicornis*, siehe Fussnote auf S. 9 der Bestimmungstabelle.

20. *Sphinginopalpus (Sphinginafricanus) tubulatus* sp. nov.

MÄNNCHEN (Abb. 124-129).

Länge 2,5 mm.

Kopf schwarz mit einer kleinen gelben, dreieckigen Makel auf dem Vorderkopf, Spitze gegen die Stirne gerichtet; Maxillarpalpen schwarz; Fühler schwärzlich, Glieder 2 und 3 gelb, 4 bis 6 leicht

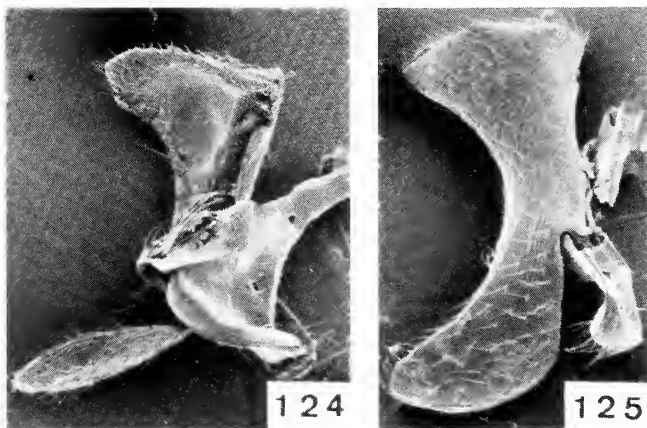


Abb. 124-125. *Sphinginopalpus* (*Sphinginafricanus*) *tubulatus* sp. nov. ♂: 124-125, Maxillarpalpen (x130) (124, von oben; 125, von unten).

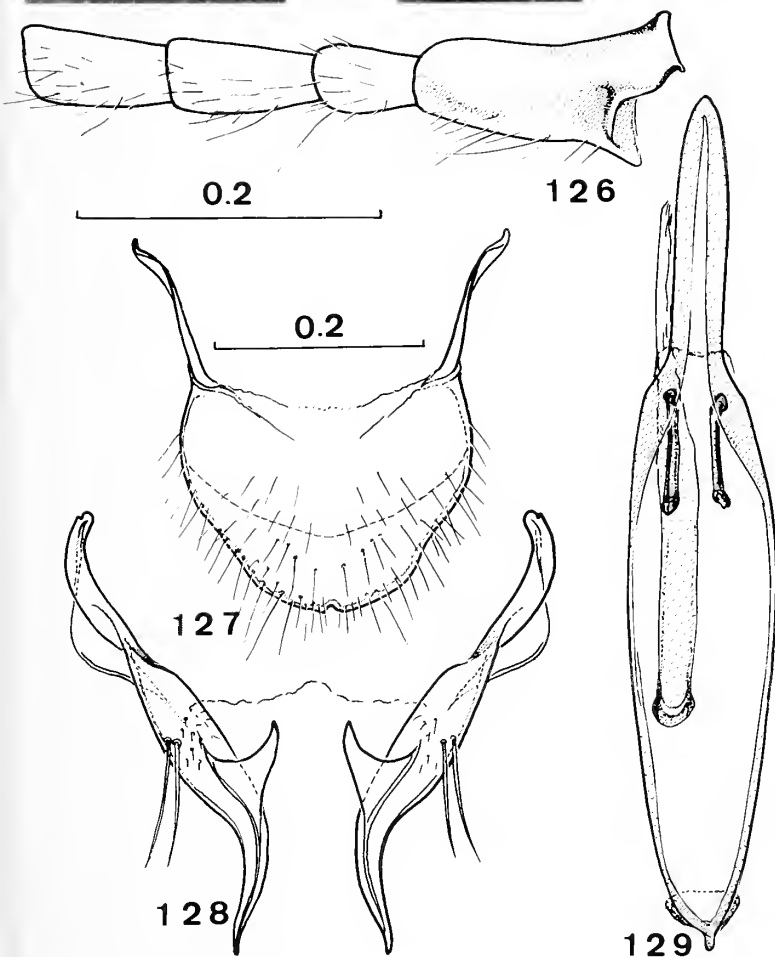


Abb. 126-129. *Sphinginopalpus* (*Sphinginafricanus*) *tubulatus* sp. nov. ♂: 126, Fühlerglieder 1-4; 127, Tergit 8; 128, Sternit 8; 129, Kopulationsapparat (dorsal). Massstab von 126 auch für 128, 129.

angedunkelt; Halsschild schwarz, Basis ein wenig aufgehell; Schildchen, Flügeldecken und Beine schwarz, alle Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert, teils fast glatt. Maxillarpalpen Abb. 124-125. Fühler (Abb. 126) ungefähr so lang wie die Flügeldecken, Glied eins 2 1/2 mal so lang wie 2, 3 bis 10 zur Spitze nur ganz schwach verbreitert, fast parallel. Halsschild ungefähr in der Mitte am breitesten; abgeflachter Teil etwas deutlicher chagriniert als der vordere, sonst wie bei *curvipalpis*. Flügeldecken wie bei *curvipalpis*, falsche Epipleuren ohne Krenulierung. Tergit 8 Abb. 127. Sternit 8 Abb. 128.

Kopulationsapparat Abb. 129 dorsal.

Holotypus (TMP): South Africa, Natal Middld.: Karkloof, intersept. trap 10 days, 1300 m, 29°18'S, 30°13'E, 2.xii.1989, E-Y:2729, S. Endrödy-Younga, I. Klimaszewski.

Die stark ausgeschnittenen Seiten von Glied 3 der Maxillarpalpen erinnern an *curvipalpis*, doch sind die Terminalia und der Kopulationsapparat mit den parallen Innenteilen sehr verschieden.

21. *Sphinginopalpus (Sphinginafricanus) natalensis* sp. nov.

MÄNNCHEN (Abb. 130-136).

Länge 2,7 mm.

Kopf schwarz, von der Mitte der Augen nach vorne gelb; Maxillarpalpen schwarz; Fühler schwarz, Glied 1 gelb mit einem schwarzen Längswisch auf der Oberseite, seltener ganz gelb, 2 bis 5 weitgehend gelb; Halsschild schwarz, Basis nicht sehr breit gelbbraun; Schildchen, Flügeldecken und Beine schwarz, nur die Tarsen gelb.

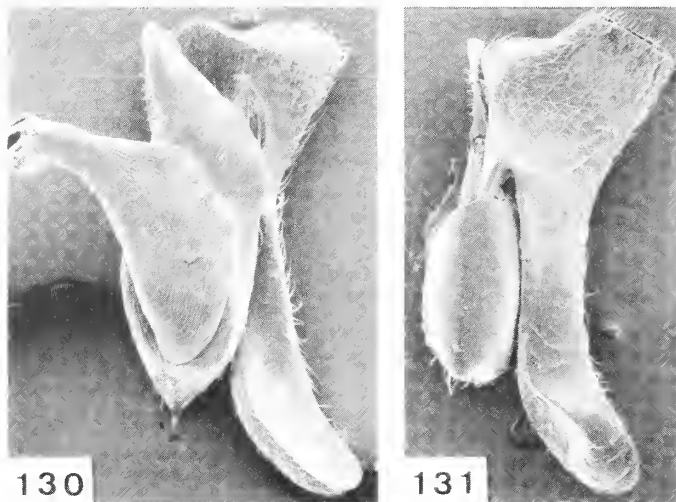


Abb. 130-131. *Sphinginopalpus (Sphinginafricanus) natalensis* sp. nov. ♂: 130-131, Maxillarpalpen (x130) (130, von oben; 131, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 130-131. Fühler (Abb. 132) ungefähr so lang wie die Flügeldecken, Glied 1 sechs mal so lang wie 2, 3 bis 10 am Innenrand ganz schwach gerundet. Halsschild länger als breit (21x17), sonst wie bei *curvipalpis*, Flügeldecken wie bei *curvipalpis*, jedoch falsche Epipleuren deutlich krenuliert. Tergit 8 Abb. 133. Sternit 8 Abb. 134.

Kopulationsapparat Abb. 135 dorsal, Abb. 136 Profil.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

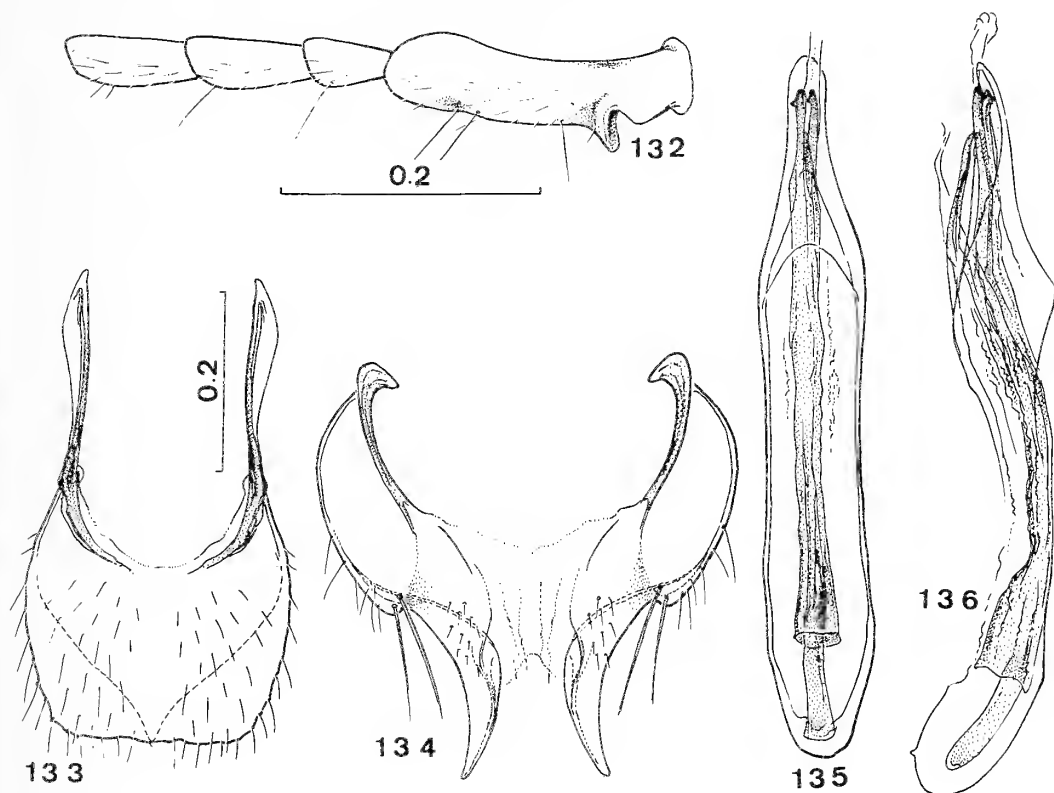


Abb. 132-136. *Sphinginopalpus (Sphinginafricanus) natalensis* sp. nov. ♂: 132, Fühlerglieder 1-4; 133, Tergit 8; 134, Sternit 8; 135-136, Kopulationsapparat (135, dorsal; 136, Profil). Massstab von 132 auch für 134 und 133 auch für 135, 136.

WEIBCHEN.

Kopf ganz schwarz; Fühler dunkel, erste 4 bis 5 Glieder gelb, oder 1 auf der Oberseite schmal angedunkelt, sonst wie das ♂ gefärbt. Flügeldecken wie bei *repandus*; ungeflügelt.

Holotypus und 7 Paratypen (TMP), 5 Paratypen (NHMB): South Africa, Natal Middld.: Karkloof grassveld with river, 29°19'S, 30°15'E, 7.-9.xii.1989, E-Y:2737, 2747, 2749, 2753, 2758, S. Endrödy-Younga, I. Klimaszewski; Doreen Clark Nature Reserve, beating in forest, 29°34'S, 30°17'E, 8. und 11.xii.1989, E-Y:2750, 2760, S. Endrödy-Younga, I. Klimaszewski, 3 Paratypen (TMP), 2 Paratypen (NHMB).

Neben *recurvus* Wittmer zu stellen.

22. *Sphinginopalpus (Sphinginafricanus) obtusodentatus* sp. nov.

MÄNNCHEN (Abb. 137-143).

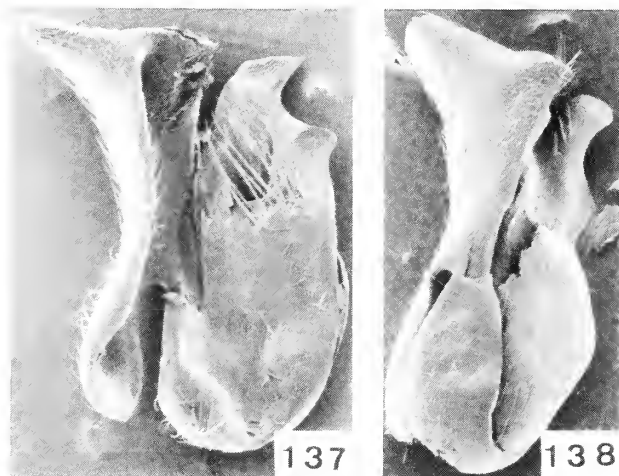


Abb. 137-138. *Sphinginopalpus (Sphinginafricanus) obtusodentatus* sp. nov. ♂: 137-138, Maxillarpalpen (x130) (137, von oben; 138, von unten).

Länge ca. 2,3 mm.

Kopf schwarz, von der Mitte der Augen nach vorne gelb; Maxillarpalpen dunkelbraun; Fühler bis zu Glied 10 (11 fehlt) gelb; Halsschild dunkelbraun, Basis ziemlich breit gelb; Schildchen, Flügeldecken und Beine braun, Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 137-138. Fühler (Abb. 139) ungefähr so lang wie die Flügeldecken, Zahn auf Glied 1 breit und stumpf, 3 bis 10 am Innenrand ganz schwach gerundet. Halsschild länger als breit (21x16), sonst wie bei *curvipalpis*; Oberseite fein chagriniert. Flügeldecken wie bei *curvipalpis*.

Tergit 8 (Abb. 140), apikaler Rand umgeschlagen (auf der Abbildung durch eine punktierte Linie bezeichnet). Sternit 7 Abb. 141; Sternit 8 (Abb. 142) nur mit einer langen Borste versehen.

Kopulationsapparat Abb. 143 dorsal.

Holotypus (BM): South Africa, Natal: Malvern, ix.1897, G. A. K. Marshall, von Champion als *Sphinginopalpus collaris* (Boheman) bestimmt.

Eine neue Art die neben *tubulatus* Wittmer gestellt werden kann, Fühlerglied 1 ähnlich gebaut, jedoch mit verschieden gebauten Maxillarpalpen, Terminalia und Kopulationsapparat.

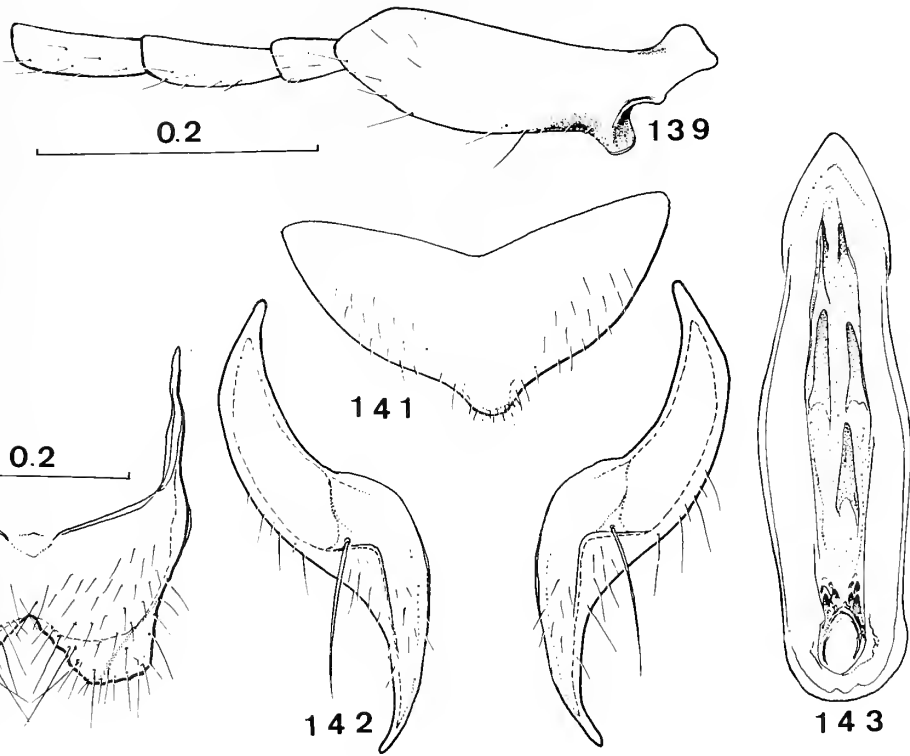


Abb. 139-143. *Sphinginopalpus (Sphinginafricanus) obtusodentatus* sp. nov. ♂: 139, Fühlerglieder 1-4; 140, Tergit 8; 141, Sternit 7; 142, Sternit 8; 143, Kopulationsapparat (dorsal).

23. *Sphinginopalpus (Sphinginafricanus) unisetosus* sp. nov.

MÄNNCHEN (Abb. 144-149).

Länge 2,5 mm.

Kopf und Maxillarpalpen schwarz; Fühler gelb, ab Glied 7 verstärkt angedunkelt, 1 mit schwarzem Längswisch auf der Oberseite; Halsschild schwarz, Basis rotbraun; Schildchen und Flügeldecken schwarz; alle Tarsen gelb, Hinterbeine schwarz, Vorder- und Mittelbeine schwarz, Knie wenig, Tibien an der Spitze breiter gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 144-145. Fühler (Abb. 146) um ca. 1/10 kürzer als die Flügeldecken, Glieder 3 bis 10 zur Spitze kaum merklich verbreitert. Halsschild länger als breit (21x16), ungefähr in der Mitte am breitesten, sonst wie bei *curvipalpis*, jedoch die Oberfläche des aufgewölbten Teiles ist

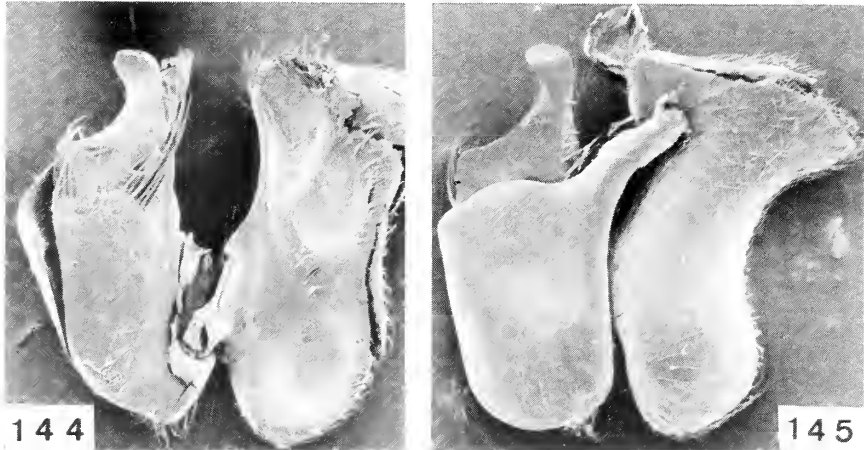


Abb. 144-145. *Sphinginopalpus (Sphinginafricanus) unisetosus* sp. nov. ♂: 144-145, Maxillarpalpen (x130) (144, von oben, Glieder 1 und 2 aufgeklappt; 145, von unten).

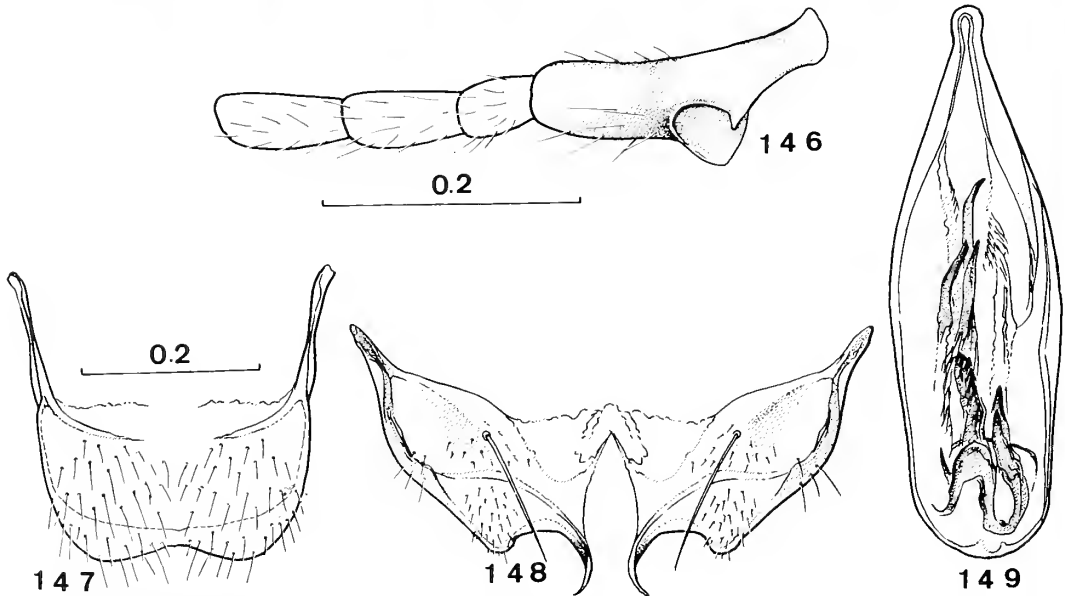


Abb. 146-149. *Sphinginopalpus (Sphinginafricanus) unisetosus* sp. nov. ♂: 146, Fühlerglieder 1-4; 147, Tergit 8; 148, Sternit 8; 149, Kopulationsapparat (dorsal). Massstab von 146 auch für 148 und 147 auch für 149.

glatt, die abgeflachte Basis feinstens chagriniert. Flügeldecken wie bei *curvipalpis*, aber etwas schwächer punktiert. Tergit 8 Abb. 147. Sternit 8 Abb. 148.

Kopulationsapparat Abb. 149 Profil.

Holotypus (NCI): South Africa, Natal: Cathedral Peak area, above Mike's Pass, 1973 m, 28°59'S, 29°14'E, 19.-23.i.1986, B. Grobbelaar.

Eine der wenigen Arten bei denen die beiden Teilstücke von Sternit 8 durch feines Gewebe lose verbunden sind, sie kann deshalb neben *natalensis* Wittmer gestellt werden. Sonst von dieser Art sehr verschieden, vergleiche mit Abb. 130-136.

24. *Sphinginopalpus* s. str. *pallidipalpis* sp. nov.

MÄNNCHEN (Abb. 150-156).

Länge gut 2 mm.

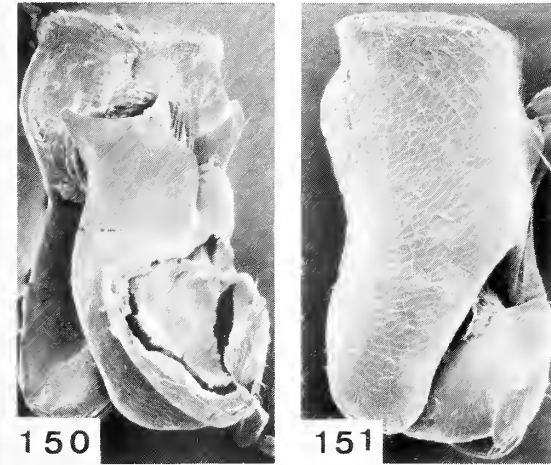


Abb. 150-151. *Sphinginopalpus* s. str. *pallidipalpis* sp. nov. ♂: 150-151, Maxillarpalpen (x170) (150, von oben; 151, von unten).

3 bis 10 zur Spitze nur ganz wenig verbreitert, 3 so lang wie 4. Halsschild länger als breit (19,5x17,5), sonst wie *capensis*. Flügeldecken langoval, falsche Epipleuren stärker herausstehend, ca. 60% der Länge einnehmend, an der breitesten Stelle ganz schwach krenuliert; Punkte etwas gröber als bei *capensis*, sonst wie diese gebaut. Tergit 8 Abb. 153. Sternit 7 Abb. 154, Sternit 8 Abb. 155.

Kopulationsapparat Abb. 156 Profil.

Holotypus (BM): South Africa, Cape Prov.: Dunbrody, 33°28'S, 25°33'E, under seeds, 6.vi.1903, O'Neil.

Diese neue Art wurde von Champion, 1922, als *oneili* Pic bestimmt. Sie gehört zu den wenigen Arten mit durchgehendem, weisslichem Querband auf den Flügeldecken und gleicht äusserlich etwas *capensis* Wittmer, doch sind bei letzterer die Flügel, der Halsschild und die Beine dunkler, nebst sehr verschieden gebautem Fühlerglied 1 und Terminalia.

Kopf gelb mit einem dunkeln Flecken an der Kopfbasis, der seitlich bis ungefähr zur Mitte der Schläfen reicht und nach vorne bis zur Mitte der Augen; Maxillarpalpen gelb; Fühler gelb, die letzten 4 bis 5 Glieder angedunkelt; Halsschild dunkelbraun, abgeflachter Teil gelbbraun; Flügeldecken dunkelbraun mit einem gelblichen Querband vor der Mitte, das an den Seiten nach hinten verlängert ist; Hinterbeine schwärzlich, alle 6 Tarsen gelb, 4 vordere Schenkel grösstenteils hell, 4 vordere Tibien gelb.

Kopf mit den Augen kaum merklich breiter als der Halsschild, Stirne leicht gewölbt, Oberfläche fein chagriniert. Maxillarpalpen Abb. 150-151. Fühler (Abb. 152) um ca. 1/10 kürzer als die Flügeldecken, Glied 1 ohne Zahn, gleich nach der Basis stark verbreitert und dann zur Spitze verschmälert,

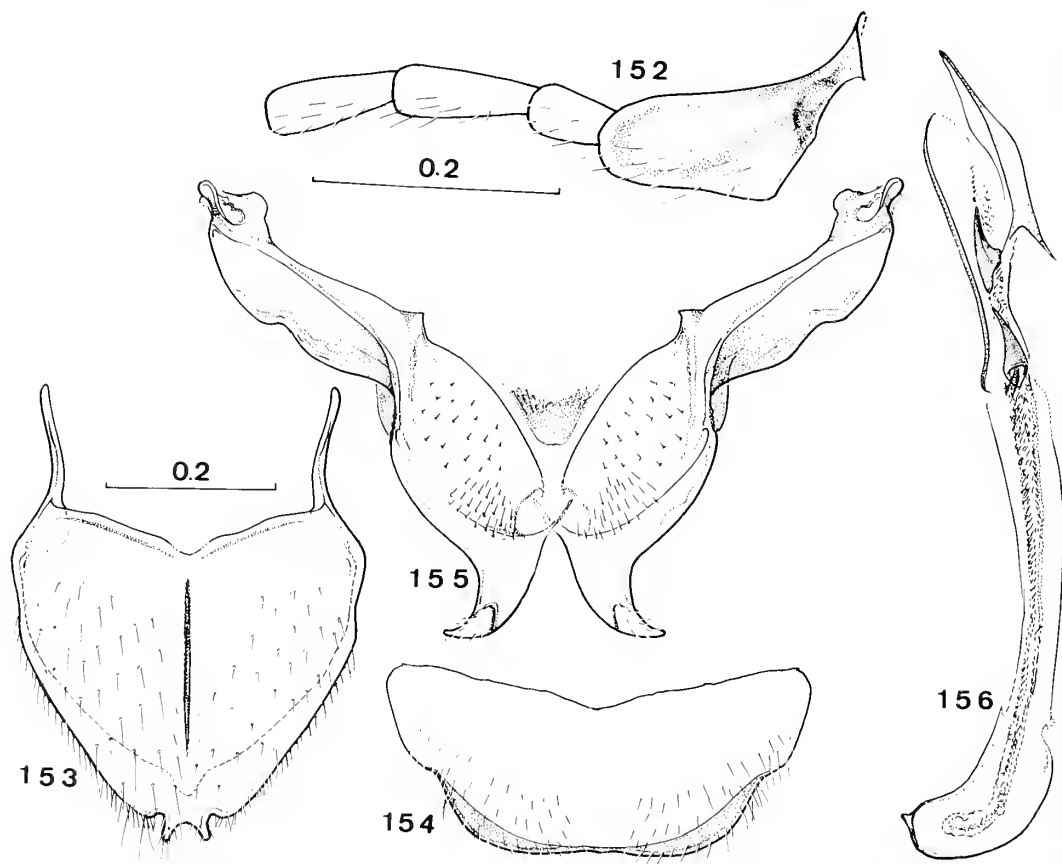


Abb. 152-156. *Sphinginopalpus* s. str. *pallidipalpis* sp. nov. ♂: 152, Fühlerglieder 1-4; 153, Tergit 8; 154, Sternit 7; 155, Sternit 8; 156, Kopulationsapparat (Profil). Massstab von 152 auch für 155, 156 und 153 auch für 154.

25. *Sphinginopalpus* s. str. *flavomarginatus* Champion

Sphinginopalpus flavomarginatus Champion, 1922: 334.

MÄNNCHEN (Abb. 157-163).

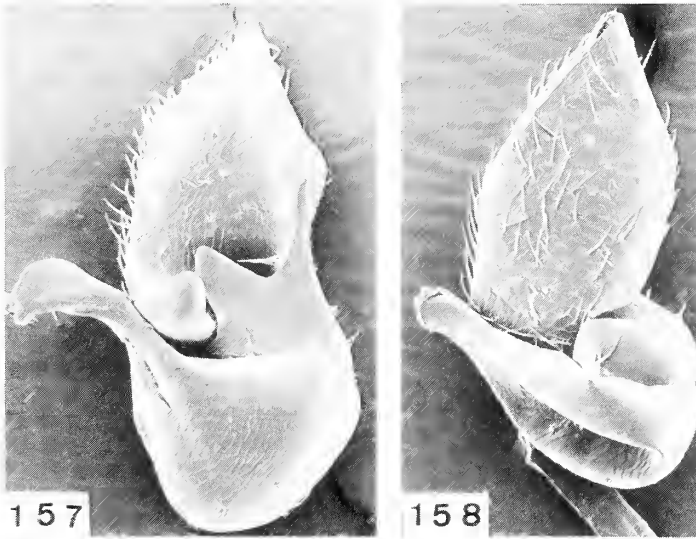


Abb. 157-158. *Sphinginopalpus* s. str. *flavomarginatus* Champion ♂: 157-158, Maxillarpalpen (x220) (157, von oben; 158, von unten).

Am Originalfundort: Frere, Natal, fing ich am 8.xi.1992, ein weiteres ♂. Für die Abbildungen wurde der Holotypus im BM verwendet. Maxillarpalpen Abb. 157-158. Fühlerglieder 1-4 Abb. 159. Tergit 8 Abb. 160. Sternit 8 Abb. 161. Kopulationsapparat Abb. 162 dorsal, Abb. 163 Profil.

Dem ganzen Aussehen nach könnte diese Art leicht in die Untergattung *Sphinginafricanus* gehören.

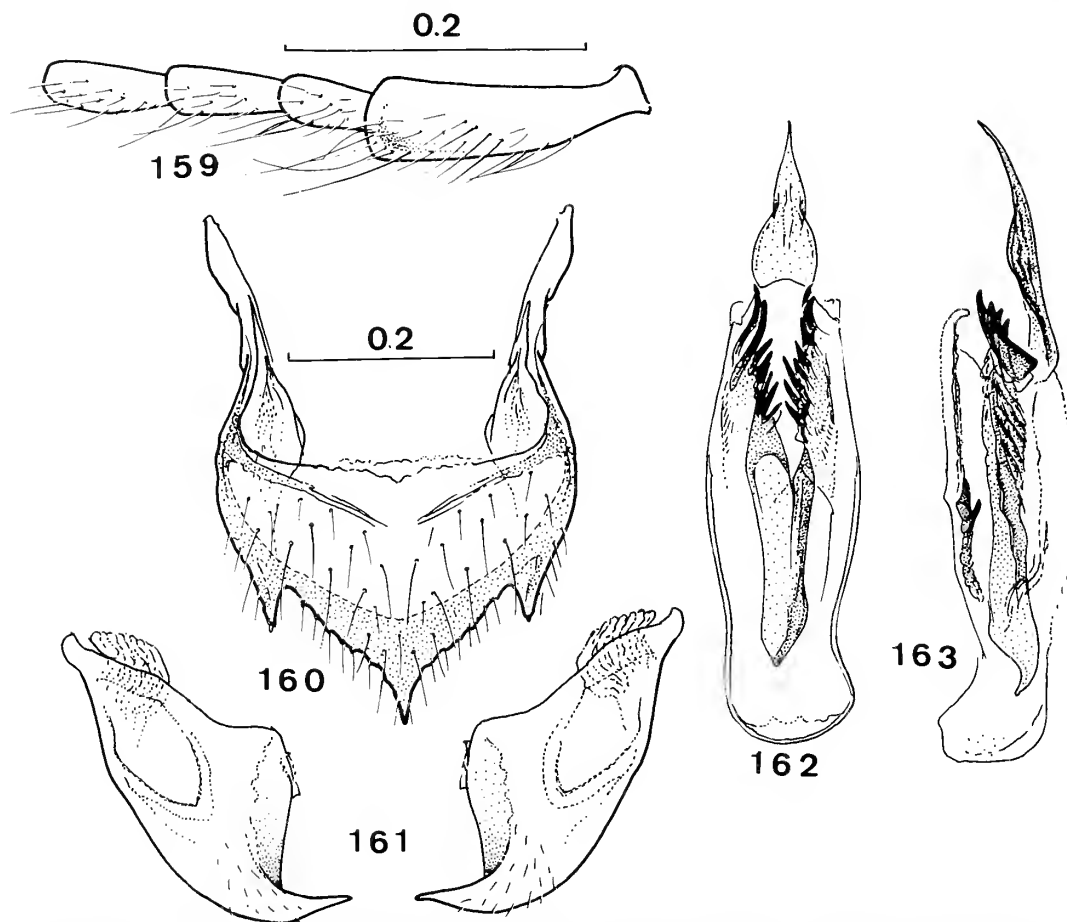


Abb. 159-163. *Sphinginopalpus* s. str. *flavomarginatus* Champion ♂: 159, Fühlerglieder 1-4; 160, Tergit 8; 161, Sternit 8; 162-163, Kopulationsapparat (162, dorsal; 163, Profil). Massstab von 159 auch für 161 und 160 auch für 162, 163.

26. *Sphinginopalpus* s. str. *triangulatus* sp. nov.

MÄNNCHEN (Abb. 164-169).

Länge 1,8 mm.



Abb. 164-165. *Sphinginopalpus* s. str. *triangulatus* sp. nov. ♂: 164-165, Maxillarpalpen (x250).

kürzer als die Flügeldecken, Glied 1 einfach, 3 deutlich länger als 2, 4 ein wenig breiter als 3. Halsschild knapp länger als breit (14x13), Seiten nach vorne fast in gerader Linie schwach verbreitert; Seitenränder besonders an der Stelle der Einschnürung stark entwickelt, erhöht, fein krenuliert; Oberfläche glatt. Flügeldecken langoval, wie bei *elongatidens*; Punktreihen bis weit nach hinten sichtbar. Tergit 8 Abb. 167. Sternit 8 Abb. 168.

Kopulationsapparat Abb. 169 dorsal.

Holotypus und 1 Paratypus ♂ (TMP), 1 Paratypus ♂ (NHMB): South Africa, Natal: Weza, Impetyene grassveld, flowering grassveld, 30°37'S, 29°42'E, 21. und 25.xi.1989, E-Y:2709, 2718, S. Endrödy-Younga, I. Klimaszewski.

Eine der wenigen Arten mit einfachem, nicht gezahntem Fühlerglied 1, neben *flavomarginatus* Champion zu stellen.

Kopf schwarz, Vorderkopf mit einem dreieckigen gelben Flecken zwischen den Fühlerwurzeln; Maxillarpalpen gelb, vorletztes Glied teilweise bräunlich; Fühler gelb, letzte 5 bis 6 Glieder schwarz; Halsschild schwarz, abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem weissen Saum jederseits, der unter den Schultern beginnt und fast bis zur Spitze reicht; Hinterschenkel dunkel, auf der Unterseite aufgeheilt, die 4 vorderen braun, Tibien und Tarsen gelblich.

Kopf mit den Augen so breit wie der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 164-165. Fühler (Abb. 166) fast um 1/3

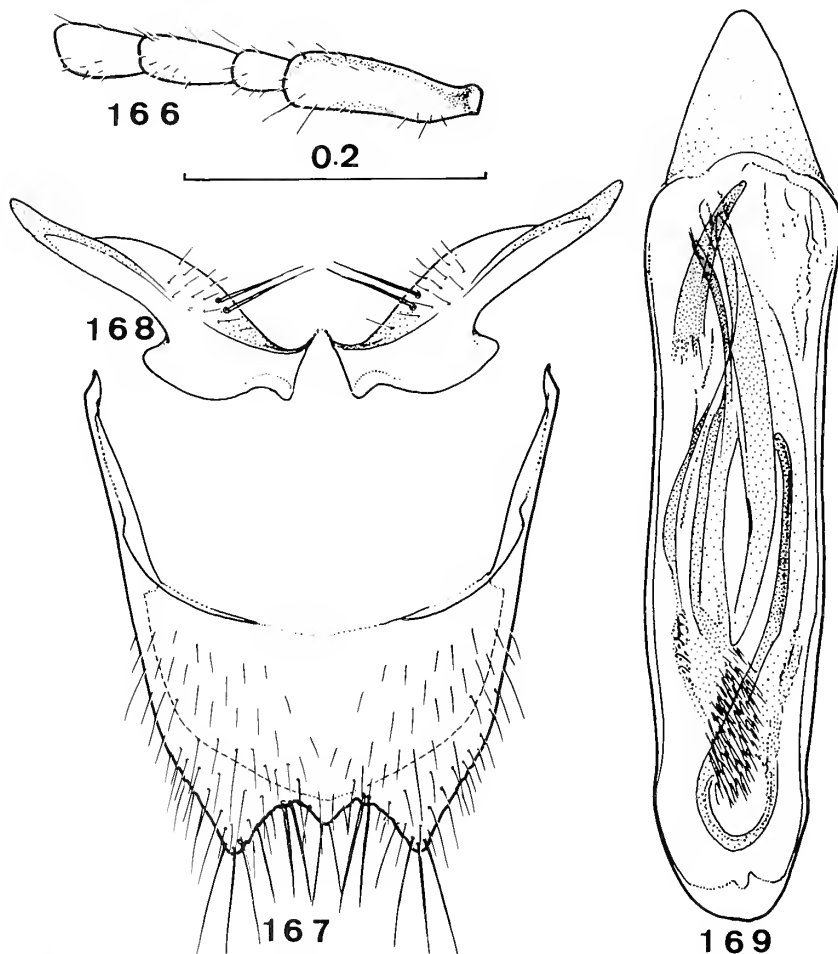


Abb. 166-169. *Sphinginopalpus* s. str. *triangulatus* sp. nov. ♂: 166, Fühlerglieder 1-4; 167, Tergit 8; 168, Sternit 8; 169, Kopulationsapparat (dorsal). Massstab von 166 auch für 167-169.

27. *Sphinginopalpus* s.str. *orientalis* sp. nov.

MÄNNCHEN (Abb. 170-180).

Länge 2-2,2 mm.

Gelb, orange und braun; Kopf an der Stirne zwischen den Augen oft leicht angedunkelt; Fühler und Maxillarpalpen gelb bis orange; Halsschild und Schildchen braun; Flügeldecken ebenso, auf der hinteren Hälfte ein grosser, dunkler, isolierter Flecken, der an der Naht manchmal ein wenig aufgelöst ist, oft befindet sich eine kleine, kurze Verdunkelung auf der angedeuteten Rippe hinter den Schulterbeulen; Beine hellbraun, Hinterschienen leicht angedunkelt.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

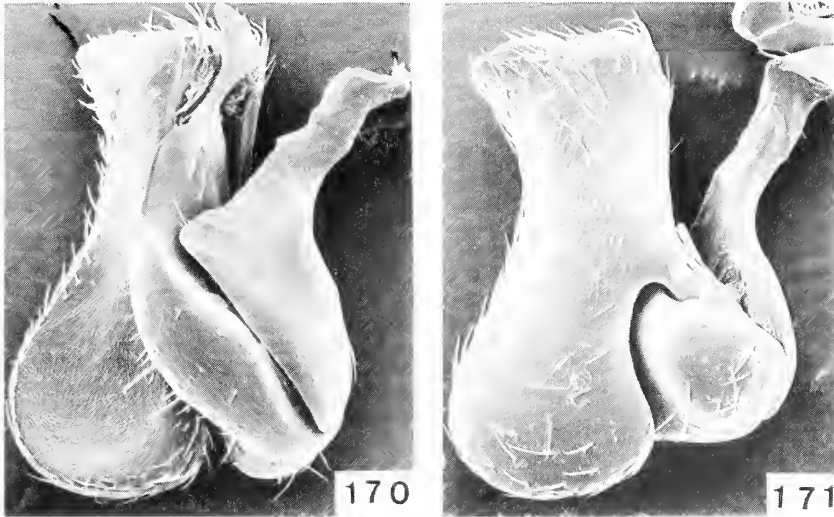


Abb. 170-171. *Sphinginopalpus* s. str. *orientalis* sp. nov. ♂: 170-171, Maxillarpalpen (x220) (170, von oben; 171, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 170-171. Fühler (Abb. 172) ca. 10% länger als die Flügeldecken, Glied 1 mit einer kurzen Kerbe gleich nach der Basis und anschliessend mit einem ziemlich langen, schmalen, spitzen Zahn; folgende Glieder schmal. Halsschild länger als breit (16x12), Seiten gerundet und anschliessend gegen die Basis gerundet verengt; Chagriniierung des aufgewölbten Teils fein, auf dem verengten Teil nur wenig stärker. Flügeldecken ca. doppelt so lang wie der Halsschild, nach hinten verbreitert, hinter den Schulterbeulen eine kurze angedeutete Leiste, Punktierung grob, wenig tief, zuerst in Reihen, hinten zerstreut. Hinterschienen gekrümmt, schwach verbreitert. Tergit 8 Abb. 173. Sternit 8 Abb. 174. Spiculum Abb. 175.

Kopulationsapparat Abb. 176 dorsal.

WEIBCHEN.

Wie das ♂ gefärbt, aber die kleinen Flecken auf den Rippen der Flügeldecken fehlen manchmal. Letztes Glied der Maxillarpalpen länglich, fast oval. Fühler einfach.

Holotypus und 18 Paratypen (NHMB), 2 Paratypen (NCI), 2 Paratypen (AMG): South Africa, Natal: St Lucia, 10 m, 25.-27.x.1981, J. & S. Klapperich. Zululand: Dukuduku Forest Station, 28°22'S, 32°19'E, 5.iv.1974, E-Y:327, S. Endrödy-Younga, 2 Paratypen (TMP). Cape Prov.: De Rust Valley, 29.xi.1981, J. & S. Klapperich, Fundort wahrscheinlich unrichtig.

Diese neue Art gehört zur kleinen Gruppe mit braunem bis orangenem Halsschild (*lesothoensis*, *tetrastigma*, *hanglipensis*, *rufithorax*). Sie unterscheidet sich von diesen Arten gemäss der Bestimmungstabelle.

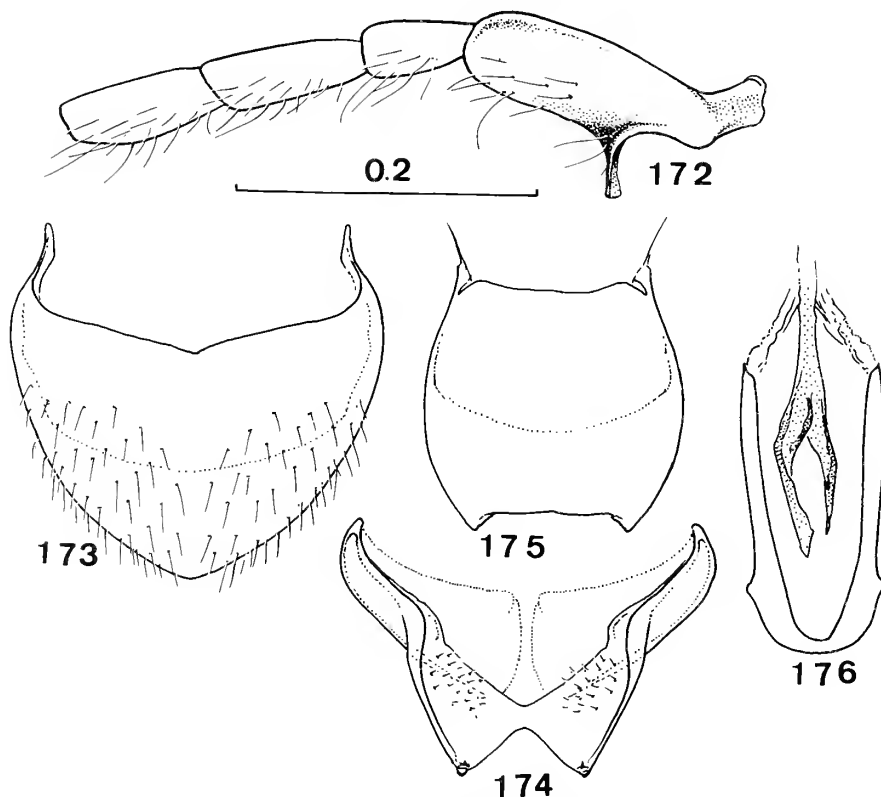


Abb. 172-176. *Sphinginopalpus* s. str. *orientalis* sp. nov. ♂: 172, Fühlerglieder 1-4; 173, Tergit 8; 174, Sternit 8; 175, Spiculum; 176, Kopulationsapparat (dorsal). Massstab von 172 auch für 173-176.

28. *Sphinginopalpus* s. str. *lesothoensis* sp. nov.

MÄNNCHEN (Abb. 177-182).

Länge 2,1-2,3 mm.

Kopf und Maxillarpalpen schwarz; Fühler schwärzlich, erste 5 Glieder gelb; Halsschild braun; Schildchen schwarz; Flügeldecken braun mit einem queren schwarzen Flecken an der Basis, die Seiten nicht erreichend, an der Naht gegen das Schildchen schwach aufgeheilt und je einem länglichen, isolierten schwarzen Flecken hinter der Mitte; Schenkel schwarz, Tibien und Tarsen braun.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 177-178. Fühler (Abb. 179) um fast 1/4 kürzer als die Flügeldecken, Glied 3 deutlich länger als 4. Halsschild kaum länger als breit (14,5x14), Seiten vorne gerundet, gegen die Basis verengt; vorderer Teil nicht sehr stark aufgewölbt; Oberfläche glatt. Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, Krenulierung fehlt; Punkte weit auseinander stehend, meistens in Reihen. Tergit 8 Abb. 180. Sternit 8 Abb. 181.

Kopulationsapparat Abb. 182 dorsal.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

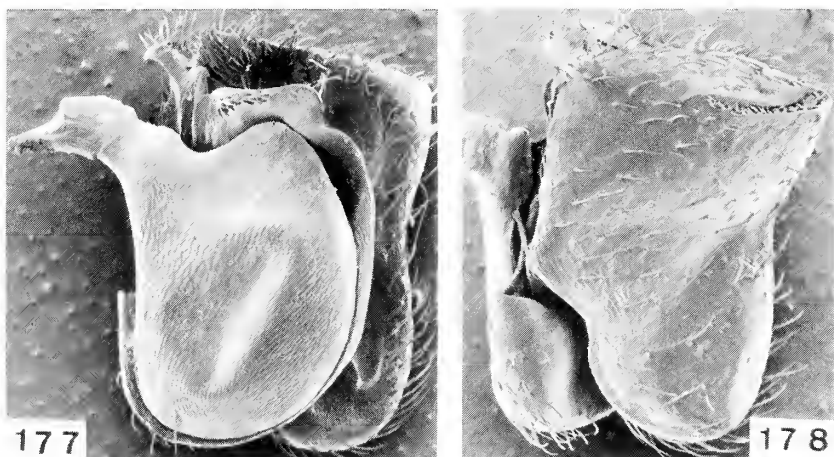


Abb. 177-178. *Sphinginopalpus* s. str. *lesothoensis* sp. nov. ♂: 177-178, Maxillarpalpen (x200) (177, von oben, 178, von unten)

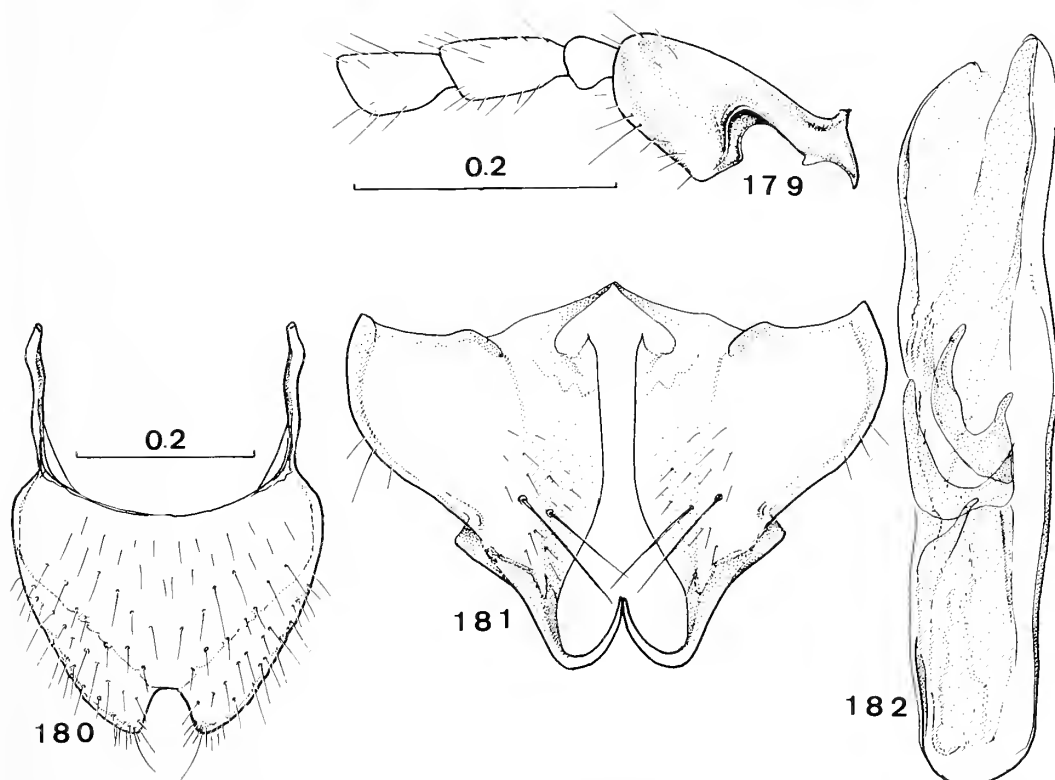


Abb. 179-182. *Sphinginopalpus* s. str. *lesothoensis* sp. nov. ♂: 179, Fühlerglieder 1-4; 180, Tergit 8; 181, Sternit 8; 182, Kopulationsapparat (dorsal). Massstab von 179 auch für 181, 182.

WEIBCHEN.

Wie das ♂ gefärbt, Fühlerglied 1 einfach.

Holotypus ♂ und 1 Paratypus ♀ (TMP): South Africa, Lesotho: Hodson's Peak, 3000 m, 28°37'S, 29°17'E, 11.iii.1976, E-Y:1068, S. Endrödy-Younga.

Neben *tetrastictus* Champion und *rufithorax* Wittmer zu stellen. Die neue Art unterscheidet sich durch die Form der Fühlerglieder 1 und 2 und die verschieden gebauten Terminalia.

29. *Sphinginopalpus* s. str. *orangensis* sp. nov.

MÄNNCHEN (Abb. 183-188).

Länge 2,2-2,5 mm.

Kopfbasis orange, Stirne zwischen dem oberen Teil der Augen mit einer breiteren dunkleren Makel, die die Augen oft berührt, Vorderkopf mit den Maxillarpalpen gelb; Fühler bis Glied 6 gelb, Oberseite von 2 und Basis von 3 leicht angedunkelt, 7 bis 11 dunkelbraun bis schwarz; Halsschild mit schmaler, fast gelber Basis, dann quer schmal dunkler, seitlich, manchmal bis zum Vorderrand dunkler, Mitte bis Vorderrand bräunlich; Schildchen dunkel, manchmal bräunlich aufgehell; Flügeldecken braun bis gelblich, jede Decke mit 2 hintereinander liegenden, ringsum isolierten braunen bis dunkelbraunen Längsmakeln; Beine gelblich bis bräunlich, besonders die Hintertibien ein wenig dunkler.

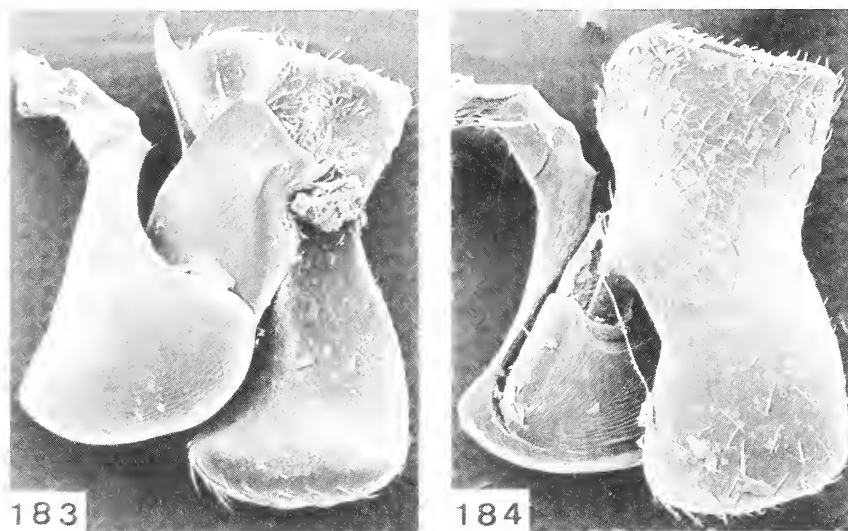


Abb. 183-184. *Sphinginopalpus* s. str. *orangensis* sp. nov. ♂: 183-184, Maxillarpalpen (x185) (183, von oben; 184, von unten).

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

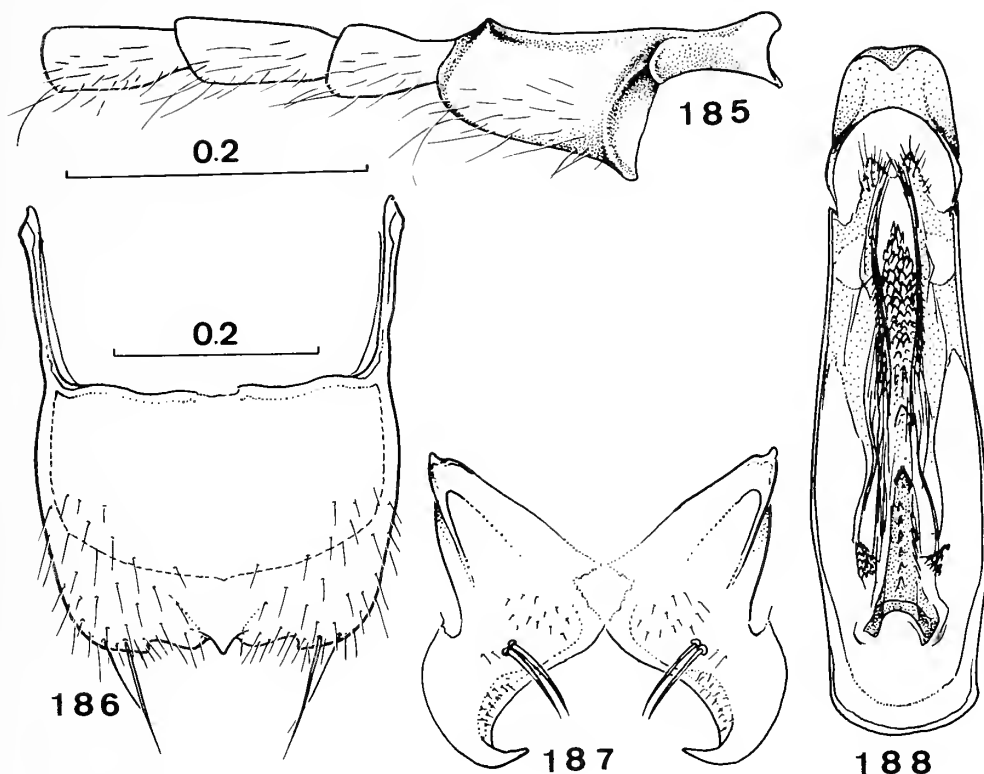


Abb. 185-188. *Sphinginopalpus* s. str. *orangensis* sp. nov. ♂: 185, Fühlerglieder 1-4; 186, Tergit 8; 187, Sternit 8; 188, Kopulationsapparat (dorsal). Massstab von 186 auch für 187-188.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; feinstens chagriniert. Maxillarpalpen Abb. 183-184. Fühler (Abb. 185) ungefähr 10% kürzer als die Flügeldecken, Glied 1 mit einer kurzen Kerbe an der Basis und einem kleinen spitzwinkligen Zahn an der Kerbe, 4 und einige folgende deutlich breiter als 3. Halsschild länger als breit (16x14), Seiten zuerst fast parallel, dann allmählich eingeschnürt; aufgewölbter Teil fast glatt bis feinstens chagriniert, dann gegen die Basis stärker chagriniert, matt. Flügeldecken ca. 2,6 mal länger als der Halsschild, nach hinten etwas verbreitert, Punktierung grob, in Reihen bis etwa 2/3 der Länge, dann weniger tief und zerstreut. Hinterschienen ein wenig gekrümmt, gegen die Spitze allmählich schwach verbreitert. Tergit 8 Abb. 186. Sternit 8 Abb. 187.

Kopulationsapparat Abb. 188 dorsal.

WEIBCHEN (Abb. F).

Kopf und Halsschild meistens etwas blasser als beim ♂. Letztes Glied der Maxillarpalpen beilförmig (Abb. F). Fühlerglieder 4 und folgende nur ganz unmerklich breiter als 2 und 3, die dunkle

Färbung an 2 und 3 nur angedeutet oder ganz fehlend. Halsschild länger (18/19x15).

Holotypus und 34 Paratypen (NHMB): South Africa, Richtersveld: Alexander Bay, river, 28°32'S, 16°33'E, 6.-7.ix.1987; idem E-Y: 2478, S. Endrödy-Younga, 56 Paratypen (TMP), 4 Paratypen (AMG).

Von den übrigen Arten mit braunem bis orangenem Halsschild unterscheidet sich diese Art durch den mehr oder weniger stark leicht dunkel gefleckten Halsschild, das Fühlerglied 1 und die Terminalia.

30. *Sphinginopalpus s.str. tetrastigma* Champion

Sphinginopalpus tetrastigma Champion, 1922: 333.

MANNCHE (Abb. 189-194).

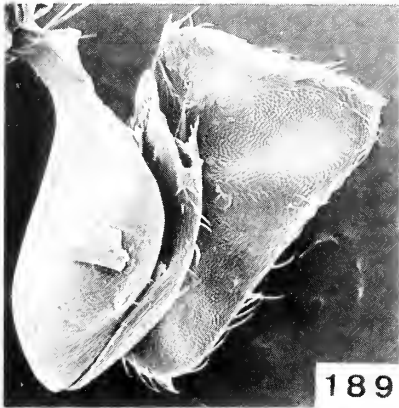


Abb. 189. *Sphinginopalpus s. str. tetrastigma* Champion ♂: 189, Maxillarpalpus (x220).

Der Holotypus befindet sich im BM, er wurde für die Abbildungen verwendet.

Das letzte Glied der Maxillarpalpen (Abb. 189) ist vorne viel stärker verbreitert als bei den folgenden 2 Arten und der Aussenrand verläuft in gerader Linie nach hinten, bei den anderen Arten ist er gerundet ausgeschnitten. Fühlerglieder 1 bis 4 (Abb. 190). Tergit 8 Abb. 191. Sternit 8 Abb. 192.

Kopulationsapparat Abb. 193 dorsal, Abb. 194 Profil.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

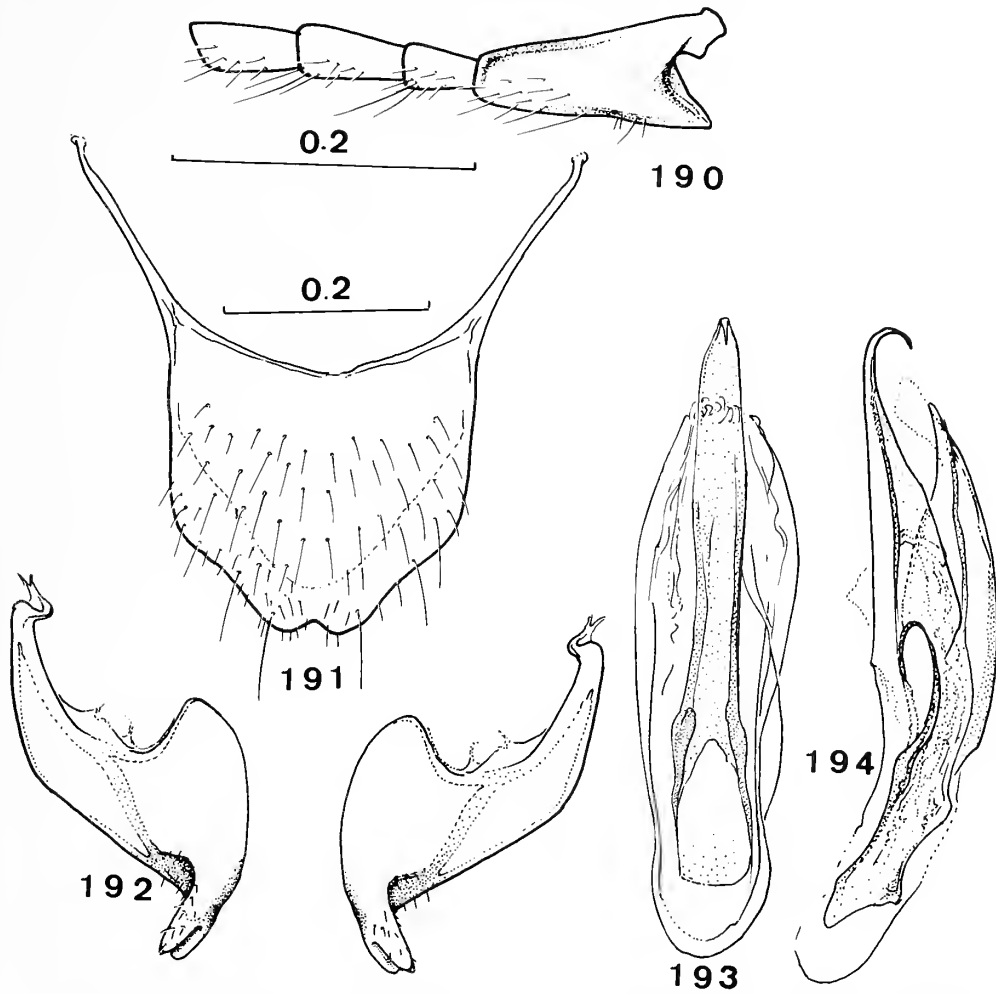


Abb. 190-194. *Sphinginopalpus* s. str. *tetrastigma* Champion ♂: 190, Fühlerglieder 1-4; 191, Tergit 8; 192, Sternit 8; 193-194, Kopulationsapparat (193, dorsal; 194, Profil). Massstab von 190 auch für 192 und 191 auch für 193, 194.

31. *Sphinginopalpus* s. str. *hanglipensis* sp. nov.

MÄNNCHEN (Abb. 195-201).

Länge 2 mm.

Kopf orange, Stirne angedunkelt, die dunkle Färbung zieht sich schmal nach vorne, bis zur Hälfte neben den Augen und Wangen orange; Maxillarpalpen, Halsschild, Schildchen und Beine orange bis hellbraun; Flügeldecken hellbraun, jede Decke mit einem basalen dunkelbraunen Flecken, beim Schildchen praktisch an die Naht anstossend, die Seiten unter den Schultern nicht erreichend und einem weiteren, länglichen, isolierten Flecken jederseits hinter der Mitte.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt, fein, mässig dicht punktiert. Maxillarpalpen Abb. 195-196. Fühler (Abb. 197) um 1/5 kürzer als die



Abb. 195-196. *Sphinginopalpus* s. str. *hanglipensis* sp. nov. ♂: 195-196, Maxillarpalpen (x230).

Flügeldecken, Glied 1 nach dem basalen Einschnitt am breitesten, gegen die Spitze regelmässig verschmälert, 3 nur wenig länger als 4, 2 bis 10 zur Spitze nur schwach verbreitert. Halsschild kaum länger als breit (15,5x14,5), vorderer Teil wenig aufgewölbt, abgeflachter Teil ebenfalls schwach gewölbt; Seiten ungefähr in der Mitte am breitesten, Randung wie bei *capensis*; ganze Oberfläche glatt, Punkte wie auf dem Kopfe. Flügeldecken langoval; falsche Epipleuren sehr lang, fast 90% der Länge einnehmend, keine Krenulierung; Punkte sehr gross, nicht sehr tief, in regelmässigen Punktreihen angeordnet; die aufrechtstehenden Haare

besonders lang. Tergit 8 Abb. 198. Sternite 7 und 8 Abb. 199.

Kopulationsapparat Abb. 200 dorsal, Abb. 201 Profil.

Holotypus (TMP): South Africa, N Transvaal: Soutpansberg, Hanglip, grassnetting, summit, 30°00'S, 29°54'E, 18.iii.1973, E-Y:68, S. Endrödy-Younga.

Eine mit *tetrastigma* Champion nahe verwandte Art, Unterschiede vergleiche Abbildungen.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

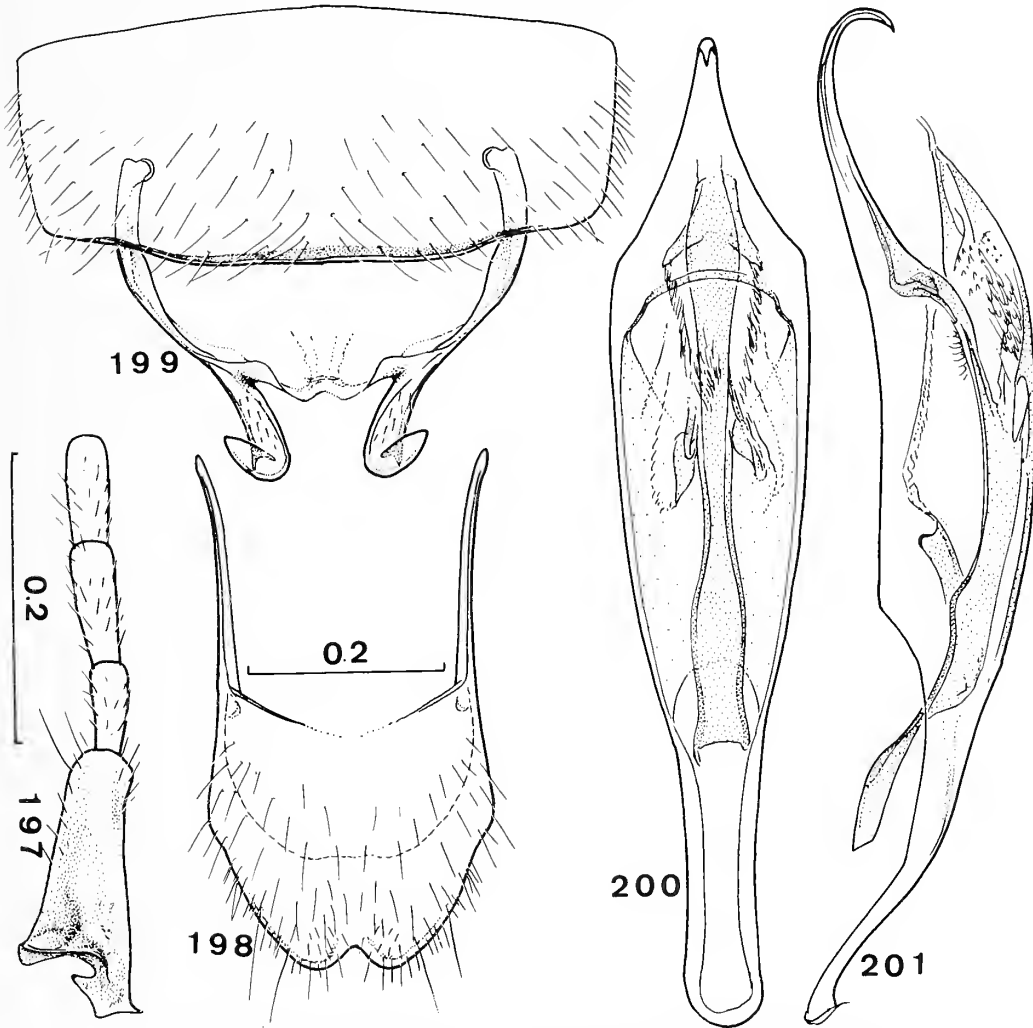


Abb. 197-201. *Sphinginopalpus* s. str. *hanglipensis* sp. nov. ♂: 197, Fühlerglieder 1-4; 198, Tergit 8; 199, Sternit 7 und 8; 200- 201, Kopulationsapparat (200, dorsal; 201, Profil). Massstab von 197 auch für 199-201.

32. *Sphinginopalpus* s. str. *rufithorax* sp. nov.

MÄNNCHEN (Abb. 202-207).

Länge 2,2 mm.

Kopf schwarz, von ca. der Mitte der Augen nach vorne gelb; Maxillarpalpen braun, teilweise angedunkelt; Fühler gelb, ab Glied 5 oder 6 zunehmend dunkel; Halsschild orangebraun; Schildchen schwarz; Flügeldecken vorwiegend gelb bis gelbbraun, Basis bis über die Schultern schwärzlich,

jedoch Seiten darunter hell, jederseits je ein ovaler isolierter Flecken beginnt kurz vor der Mitte und lässt die Spitzen breit hell, oder die dunkle Färbung ist stärker ausgebreitet, die ovalen Flecken grösser, sie verschmelzen an der Naht und sind schmaler werdend mit der dunkeln Basis verbunden, Spitzen breit hell; Schenkel mehr oder weniger angedunkelt, ebenso die hinteren Schienen, 4 Vorderschienen gelb, ebenso alle Tarsen.

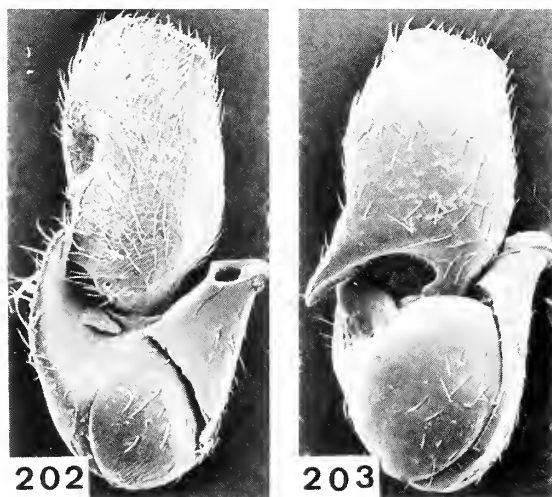


Abb. 202-203. *Sphingopalpus* s. str. *rufithorax* sp. nov. ♂: 202-203, Maxillarpalpen (x125) (202, von oben; 203, von unten)

Kopf mit den Augen nur wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt, glänzend. Maxillarpalpen Abb. 202- 203. Fühler (Abb. 204) ca. 1/4 kürzer als die Flügeldecken, Glieder 3 bis 10 nur ganz wenig zur Spitze verbreitert, 3 ein wenig länger als 4. Halsschild länger als breit (17x15), mit *capensis* übereinstimmend, jedoch vorderer Teil weniger stark aufgewölbt und Oberfläche glatt, glänzend, nur der abgeflachte Teil chagriniert. Flügeldecken langoval, ungefähr in der Mitte am breitesten, Schulterbeulen normal; falsche Epipleuren ca. 50% der Länge der Decken einnehmend, nicht krenuliert; Punktierung ähnlich wie bei *capensis*. Behaarung staubartig, auf den Flügeldecken nur ganz vereinzelte, längere, helle, aufstehende Haare. Tergit 8 Abb. 205. Sternit 8 Abb. 206.

Kopulationsapparat Abb. 207 dorsal.

WEIBCHEN.

Wie das ♂ gefärbt; Maxillarpalpen einfach.

Holotypus und 9 Paratypen (TMP), 5 Paratypen (NHMB), 1 Paratypus (AMG): South Africa, Transvaal: Waterberg, Haakdoringboom farm, flood debris, Mogo 1R, 24°11'S, 27°50'E, 13.ii.1976, E-Y:1039, A. Strydom; Onderstepoort (Pretoria), iv.1987, I. Pajor, 2 Paratypen (NHMB); Nelspruit Nature Reserve, rivulet vall., grassnetting, 19.xii.1986, 25°29'S, 30°55'E, E-Y:2402, S. Endrödy-Younga, 1 Paratypus (TMP), 1 Paratypus (NHMB).

Diese neue Art ist neben *lesothoensis* Wittmer zu stellen, mit der sie den schwarzen Kopf gemeinsam hat, Unterschiede zeigt das Fühlerglied 1 und die Terminalia, siehe Abbildungen.

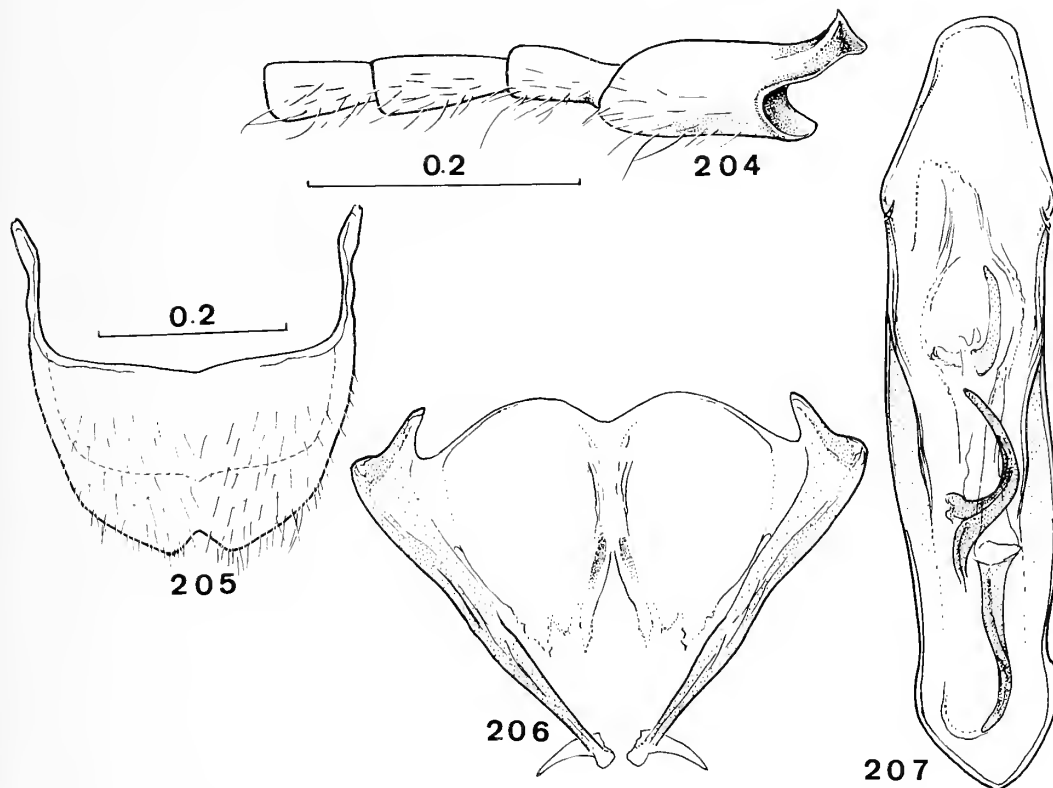


Abb. 204-207. *Sphinginopalpus* s. str. *rufithorax* sp. nov. ♂: 204, Fühlerglieder 1-4; 205, Tergit 8; 206, Sternit 8; 207, Kopulationsapparat (dorsal). Massstab von 204 auch für 206, 207.

33. *Sphinginopalpus* s. str. *nigrithorax* sp. nov.

MÄNNCHEN (Abb. 208-213).

Länge 2,3 mm.

Kopf schwarz, von der Mitte der Augen nach vorne gelb, über dem Clypeus ein kleiner, verschwommener, dunkler Flecken; Maxillarpalpen dunkel, teils aufgehellte; Fühler dunkel, erste 5 Glieder gelb, 1 und 2 auf der Oberseite schwach dunkel; Halsschild, Schildchen und Flügeldecken schwarz, letztere mit einem schmalen, weissen Querband vor der Mitte, das an der Naht schmal unterbrochen ist; Hinterbeine schwarz, Hintertibien kaum merklich aufgehellte; 4 vordere Schenkel und Tibien dunkel, Knie und Spitzen der Tibien etwas aufgehellte, 4 vordere Tarsen ziemlich hell.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 208-209. Fühler (Abb. 210) um ca. 1/5 kürzer als die Flügeldecken, Glieder 3 bis 10 fast parallel, 3 deutlich länger als 4. Halsschild länger als breit (17x14), wie bei *capensis*, jedoch aufgewölbter Teil glatt, abgeflachter Teil chagriniert. Flügeldecken lang, zur Spitze etwas verbreitert, Schulterbeulen normal; falsche Epipleuren kurz, ca. 30% der Länge einnehmend, wenig

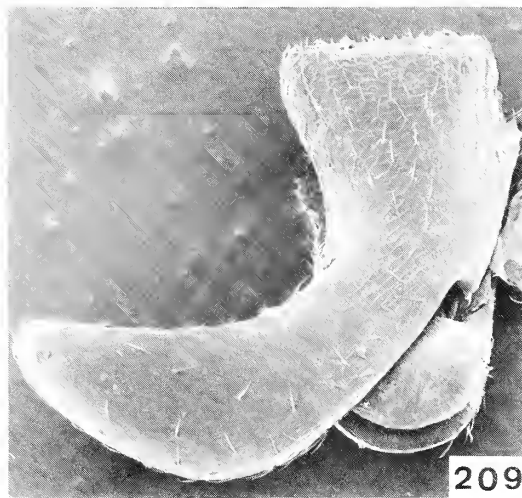
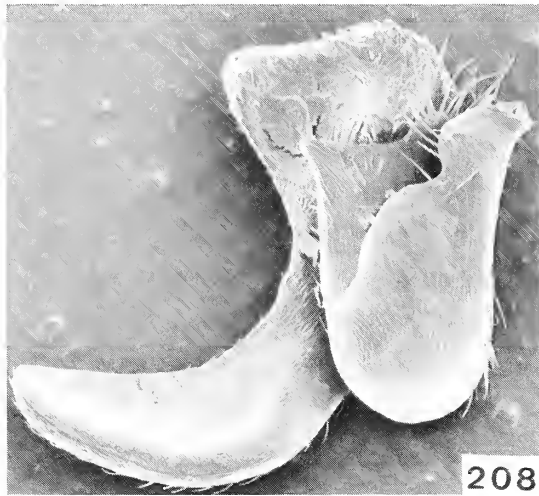


Abb. 208-209. *Sphinginopalpus* s. str. *nigrithorax* sp. nov. ♂:
Maxillarpalpen (x200) (208, von oben; 209, von unten).

vorstehend, ganz fein krenuliert; Punkte ein wenig grösser als bei *capensis*; Oberfläche glatt. Tergit 8 Abb. 211. Sternit 8 Abb. 212.

Kopulationsapparat Abb. 213 dorsal.

Holotypus (NHMB): South Africa, Cape Prov.: 2 km E Suurfontein, 22.ix.1986, W. Wittmer, M. Macpherson.

Bisher die einzige aus Südafrika bekanntgewordene Art mit einfarbig schwarzem Halsschild.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

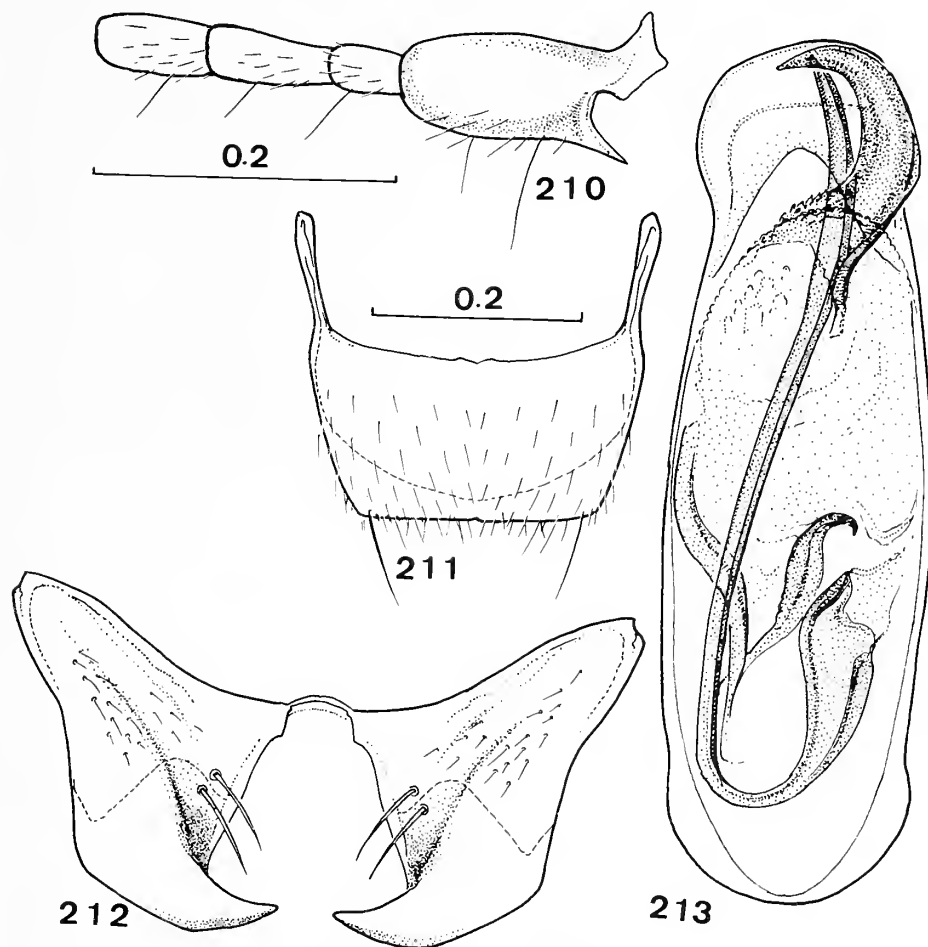


Abb. 210-213. *Sphinginopalpus* s. str. *nigrithorax* sp. nov. ♂: 210, Fühlerglieder 1-4, 211, Tergit 8; 212, Sternit 8; 213, Kopulationsapparat (dorsal). Massstab von 210 auch für 212, 213.

34. *Sphinginopalpus* s. str. *capensis* sp. nov.

MÄNNCHEN (Abb. 214-219).

Länge 1,9-2,1 mm.

Kopf schwarz mit einem breiten gelben Flecken am Vorderkopf, der selten bis zu den Augen reicht, Wangen meistens teils bis ganz gelb; Maxillarpalpen meistens gelb, seltener braun bis dunkelbraun; Fühlerglieder 1 bis 5 gelb, seltener 5 teils dunkel, restliche schwarz; Halsschild schwarz, an der Basis schmal aufgehellt; Schildchen und Flügeldecken schwarz, letztere mit einem schmalen, gelben, durchgehenden Querband vor der Mitte; Beine schwarz, Spitzen der Vordertibien seltener,

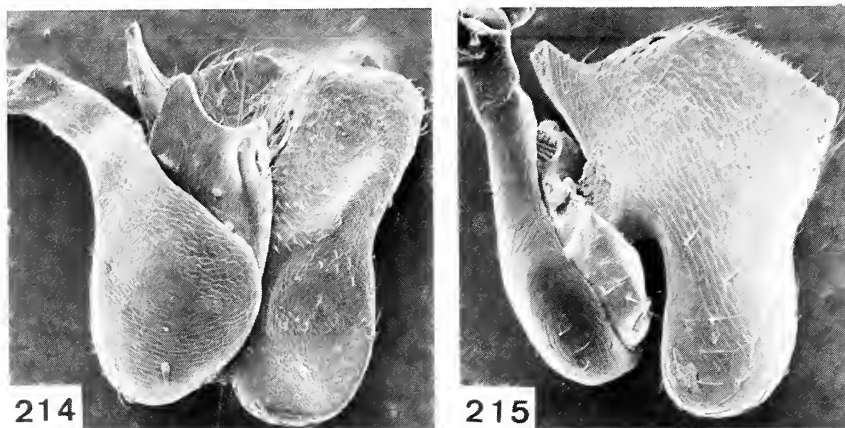


Abb. 214-215. *Spinginopalpus* s. str. *capensis* sp. nov. ♂: 214-215, Maxillarpalpen (x200) (214, von oben; 215, von unten).

Vordertarsen fast immer ganz aufgeheilt.

Kopf mit den Augen kaum merklich breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 214-215. Fühler (Abb. 216) um ca. 1/5 kürzer als die Flügeldecken, Glied 1 mit einem kleinen Zahn an der Basis oben und einem grösseren auf der Unterseite, 3 ein wenig länger als 4. Halsschild länger als breit (16x14), vorderer Teil stark aufgewölbt, Basis abgeflacht; Seiten gerundet, in der Mitte am breitesten, nach vorne kaum verschmälert, gegen die Basis stark verengt; Basalrand deutlicher als die Seitenränder, die kurz vor der Basis erlöschen; Oberfläche fein chagriniert. Flügeldecken langoval, nach der Mitte am breitesten; Schulterbeulen normal; falsche Epipleuren ca. 40% der Länge der Decken einnehmend, nur angedeutet krenuliert; Punktierung bis zur Mitte, oder darüber hinaus ziemlich grob, in Punktreihen, nach hinten erlöschend, verworren. Behaarung des Körpers fein staubartig, die Flügeldecken mit einzelnen langen, hellen, aufstehenden Haaren. Tergit 8 Abb. 217. Sternit 8 Abb. 218.

Kopulationsapparat Abb. 219 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz, sonst wie das ♂ gefärbt.

Holotypus und 6 Paratypen (NHMB): South Africa, SW Cape Prov.: 3 km S Lamberts Bay, 22.ix.1984, W. Wittmer; 50 km S Kleinsee, 30°10'S, 17°14'E, 10.ix.1987, W. Wittmer, 6 Paratypen (NHMB); 20 km N Sout Pan, 12.ix.1985, W. Wittmer, 1 Paratypus (NHMB); near Strandfontein, 31°45'S, 18°14'E, 16.ix.1986, W. Wittmer, R. Oberprieler, 28 Paratypen (NHMB), 15 Paratypen (NCI), 4 Paratypen (AMG); Papendorpdunes, 31°38'S, 18°12'E, 22.viii.1981, E-Y:1827, S. Endrödy-Younga, Paratypen (TMP); Seweputs coast, 31°39'S, 18°17'E, E-Y:1836, S. Endrödy-Younga, 8 Paratypen (TMP); Hondekliipbaai, 30°19'S, 17°17'E, 14.ix.1986, W. Wittmer, R. Oberprieler, 10 Paratypen (NHMB); 5 km E Port Nolloth, 29°17'S, 16°55'E, 9.ix.1986, W. Wittmer, R. Oberprieler, 20 Paratypen (NHMB), 3 Paratypen (NCI).

Diese neue Art ist neben *pallidipalpis* Wittmer zu stellen.

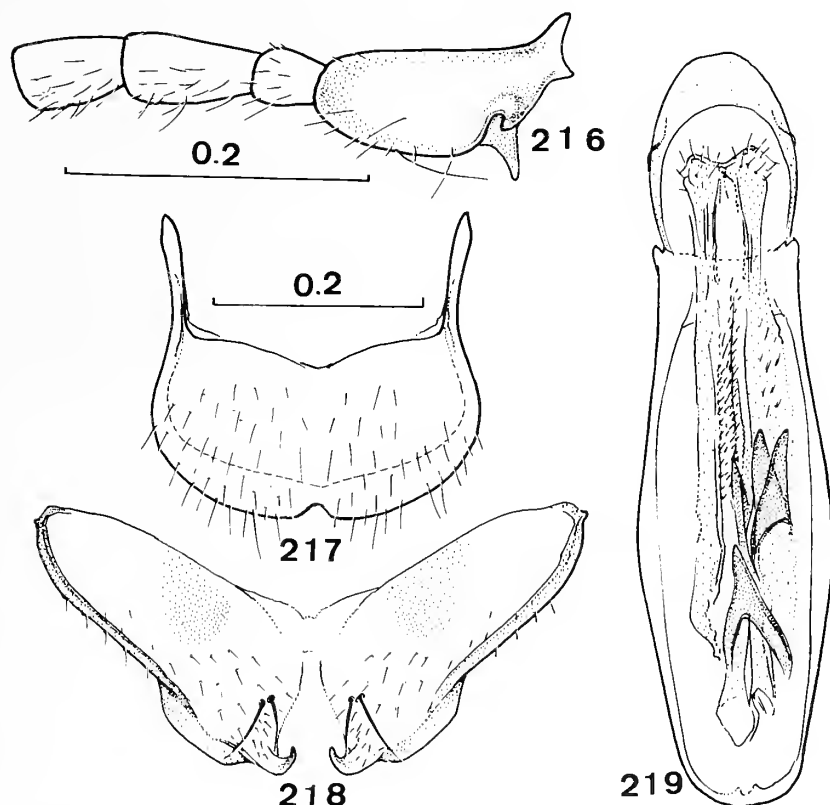


Abb. 216-219. *Sphinginopalpus* s. str. *capensis* sp. nov. ♂: 216, Fühlerglieder 1-4; 217, Tergit 8; 218, Sternit 8; 219, Kopulationsapparat (dorsal). Massstab von 216 auch für 218, 219.

35. *Sphinginopalpus* s. str. *dentifrons* sp. nov.

MÄNNCHEN (Abb. 220-226).

Länge 2,5 mm.

Kopf schwarz, von der Mitte der Augen nach vorne zuerst braun aufgehell, dann inklusive Wangen gelb; Halsschild schwarz, Maxillarpalpen gelbbraun; Fühler schwärzlich, Glieder 1 und 2 gelb, 3 bis 5 hellbraun; Halsschild schwarz, ungefähr die Hälfte des abgesetzten Teils an der Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem weisslichen, antimedialen, dreieckigen Seitenfleck, der sich etwas mehr nach hinten als nach vorne verlängert und die Naht nicht erreicht; Hinterbeine schwarz, Mittelbeine dunkelbraun, Mitteltarsen ein wenig heller,

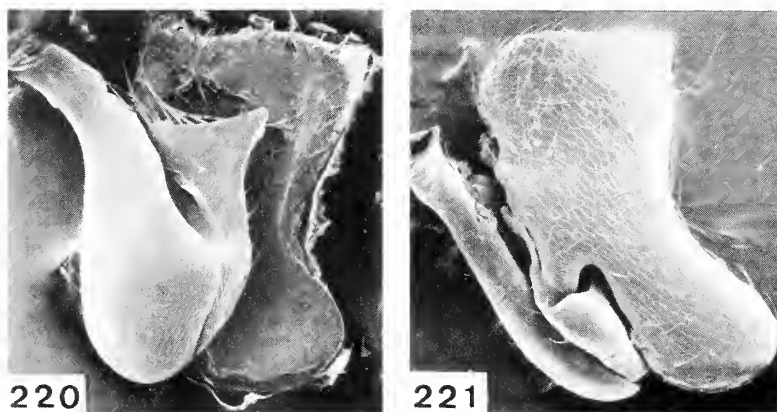


Abb. 220-221. *Sphinginopalpus* s. str. *dentifrons* sp. nov. ♂: 220-221, Maxillarpalpen (x170) (220, von oben; 221, von unten).

Vorderschenkel dunkel, bei den Knien heller, Vordertibien und Tarsen hellbraun.

Kopf (Abb. 222) mit den Augen breiter als der Halsschild; Vorderstirne mit einem kleinen, spitzen Zahn in der Mitte; Oberfläche glatt. Maxillarpalpen Abb. 220-221. Fühler (Abb. 223) um ca. 15% kürzer als die Flügeldecken, Glied 3 deutlich länger als 4. Halsschild länger als breit (20x18); Seiten nach vorne kaum merklich verengt; Oberfläche vorne glatt, abgeflachter Teil zum grössten Teil chagriniert. Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, nicht krenuliert; 2 Punktreihen neben der Naht auf 1/3 der Länge regelmässig, nach hinten nehmen die Punkte an Tiefe und Dichte ab. Tergit 8 Abb. 224. Sternit 8 Abb. 225.

Kopulationsapparat Abb. 226 dorsal.

Holotypus (TMP): South Africa, Natal: Indumeni For., Bergville Distr., humus, x.1960, N. Leleup.

Die einzige bis jetzt bekanntgewordene Art, deren Vorderstirne mit einem kleinen, spitzen Zahn bewehrt ist.

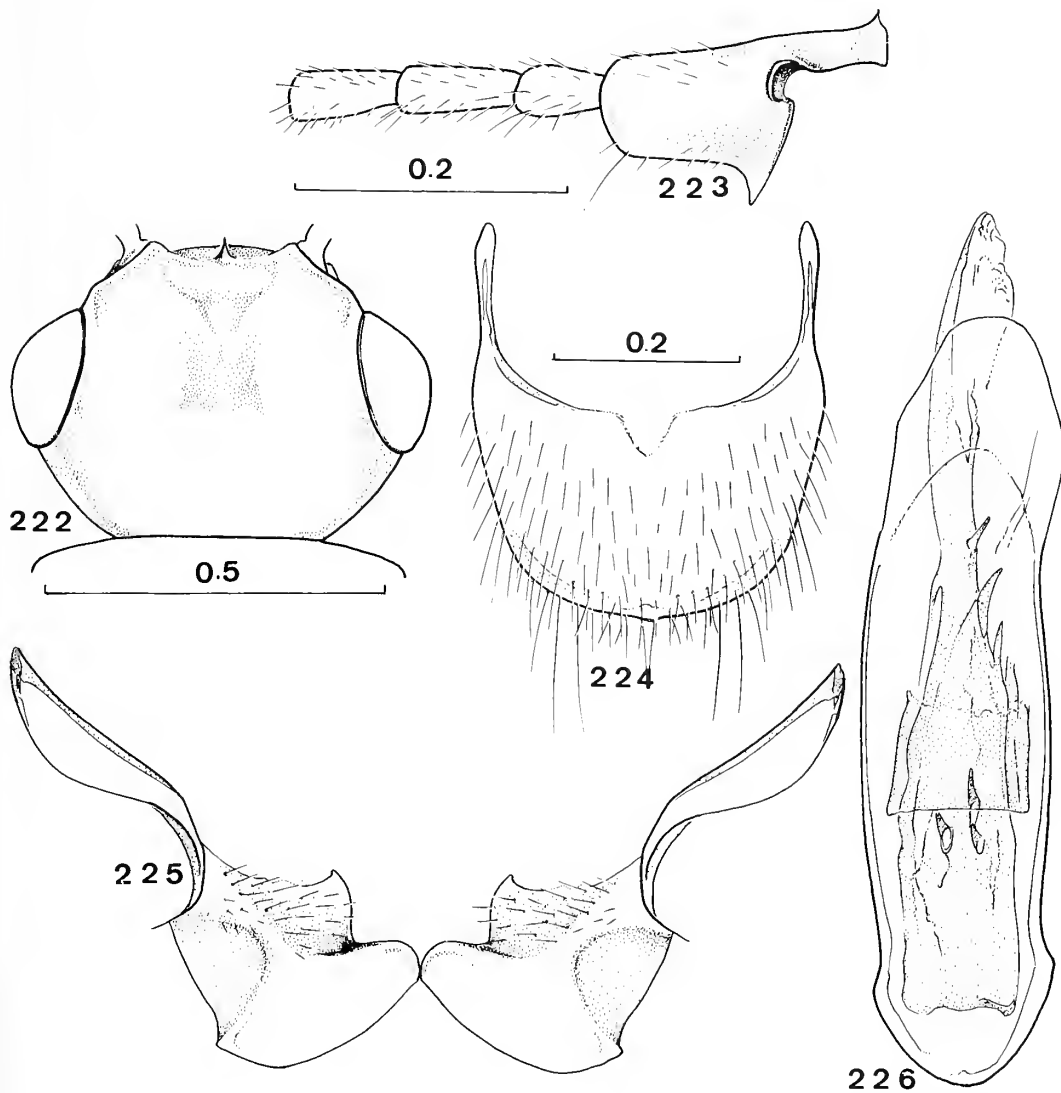


Abb. 222-226. *Sphinginopalpus* s. str. *dentifrons* sp. nov. ♂: 222, Kopf; 223 Fühlerglieder 1-4; 224, Tergit 8; 225, Sternit 8; 226, Kopulationsapparat (dorsal). Massstab von 223 auch für 225, 226.

36. *Sphinginopalpus s. str. variceps* sp. nov.

MÄNNCHEN (Abb. 227-232).

Länge 2 mm.



227



228

Abb. 227-228. *Sphinginopalpus s. str. variceps* sp. nov. ♂: 227-228, Maxillarpalpen (x200) (227, von oben; 228, von unten).

Kopf schwarz, Vorderkopf mit den Wangen variabel gelb bis orange gefärbt, manchmal beginnend am Vorderrand der Augen, oder etwas weiter vorne ein dunkles gebogenes Querband, beginnend am Vorderrand der Fühlerwurzel, in allen Fällen sind die Wangen hell; Maxillarpalpen gelb; Fühler gelb, die letzten 5 bis 6 Glieder zunehmend dunkel, bei einem Exemplar ein dunkler Längswisch auf 1 basal; Halsschild schwarz, grösster Teil der abgeflachten Basis hell; Schildchen und Flügeldecken schwarz, letztere jederseits vor der Mitte mit einem kleinen, weisslichen Flecken; Hinterbeine schwarz, Hintertibien manchmal leicht aufgehellt, 4 Vorderbeine gelb, Schenkel bis kurz vor den Knien schwarz, alle 6 Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt, einige zerstreute, feine Haarpunkte sichtbar. Maxillarpalpen Abb. 227-228. Fühler (Abb. 229) fast um 1/3 kürzer als die Flügeldecken, Glieder 3 bis 10 gegen die Spitze kaum erweitert, 3 so lang oder ein wenig länger als 4. Halsschild ungefähr so lang wie breit, sonst wie bei *capensis*, jedoch Oberfläche glatt, nur die abgeflachte Basis chagriniert. Flügeldecken langoval, wie bei *capensis*, aber stärker punktiert, falsche Epipleuren ca. 50% der Länge einnehmend, praktisch nicht krenuliert. Tergit 8 Abb. 230. Sternit 8 Abb. 231.

Kopulationsapparat Abb. 232 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz, ebenso die Maxillarpalpen, sonst wie das ♂ gefärbt.

Holotypus und 14 Paratypen (TMP), 9 Paratypen (NHMB), 2 Paratypen (AMG): South Africa, E Transvaal: Nelshoogte Forest Station, 1.- 7.xii.1986, 8.iv.1987, 25°47'S, 30°49'E, grassnetting, E-Y: 2335, 2338, 2350, 2360, 2456, S. Endrödy-Younga; Cycas Farm, grassnetting, 5.xi.1985, E-Y: 2262, S. Endrödy-Younga, 1 Paratypus (NHMB). Natal: Richards Bay, dense grass, 28°50'S, 32°05'E, 13.x.1984, P. E. Reavell, 1 Paratypus (TMP).

Diese neue Art ist neben *albilabris* (Boheman) zu stellen. Sie ist von gleicher Färbung (ausgenommen der Kopf) und Körperform, das Fühlerglied 1 ist etwas verschieden gebaut, weitere grosse Unterschiede zeigen die Terminalia, vergleiche Abbildungen.

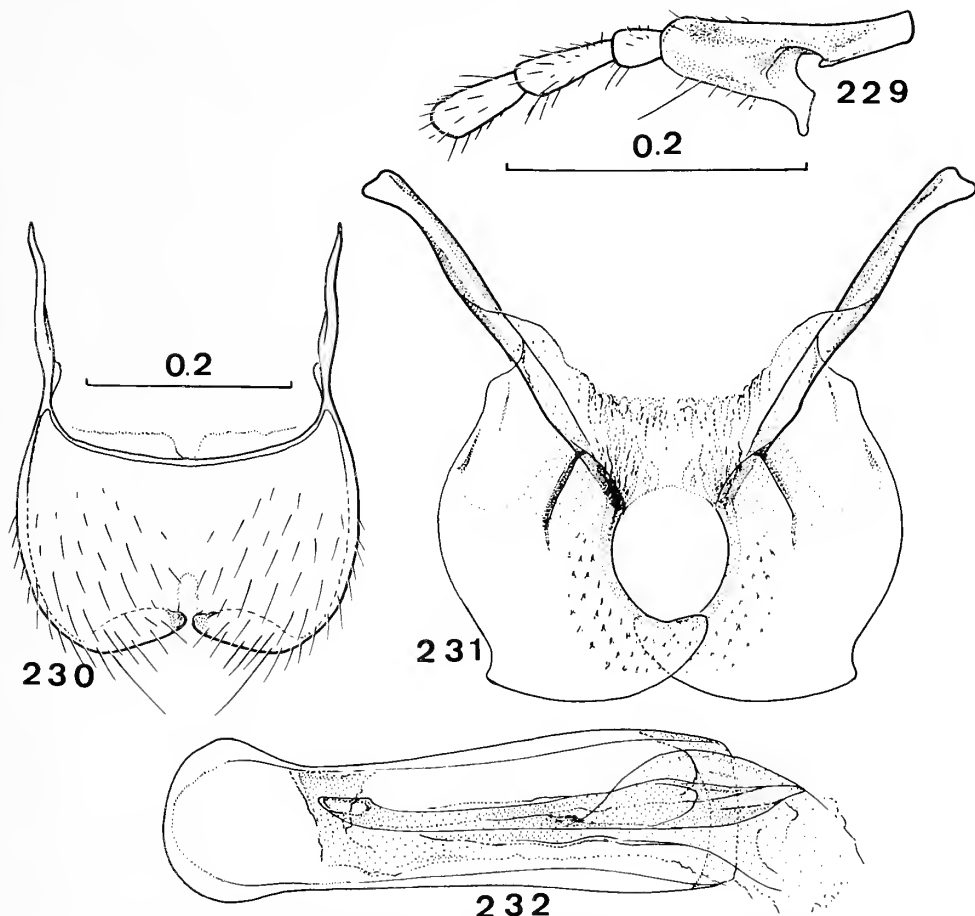


Abb. 229-232. *Sphinginopalpus* s. str. *variceps* sp. nov. ♂: 229, Fühlerglieder 1-4; 230, Tergit 8, 231, Sternit 8; 232, Kopulationsapparat (dorsal). Massstab von 229 auch für 231, 232.

37. *Sphinginopalpus* s. str. *albilabris* (Boheman)

Chalicorus albilabris Boheman, 1851: 477.

Sphinginopalpus albilabis Boheman - Champion 1922: 332, parte.

MÄNNCHEN (Abb. 233-239).

Der Holotypus (♂) stimmt mit Exemplaren überein, die mir von mehreren Fundorten vorliegen. Für die Abbildungen wurde 1 Ex. von Weza, Impetyene, E-Y:2680, verwendet: Maxillarpalpen Abb. 233-234. Fühler Abb. 235. Tergit 8 Abb. 236. Sternit 8 Abb. 237. Kopulationsapparat Abb. 238 dorsal, Abb. 239 Profil.

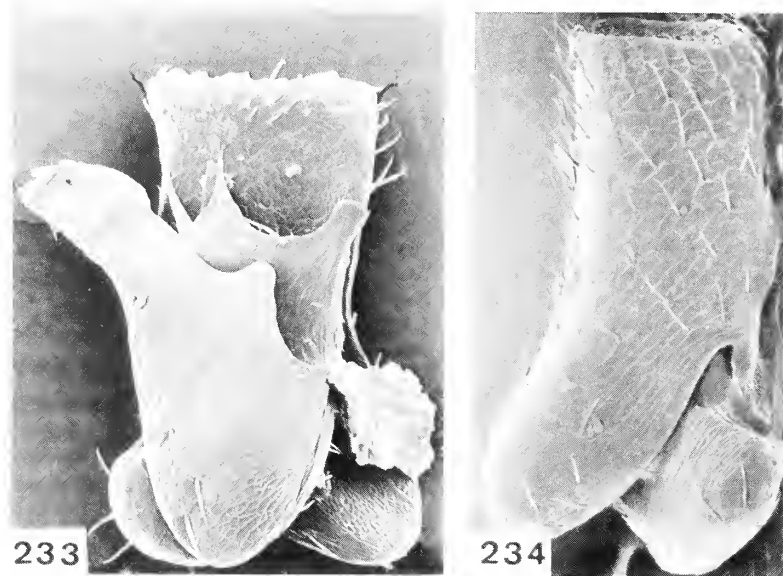


Abb. 233-234. *Sphinginopalpus* s. str. *albilabris* (Boheman) ♂: 233-234, Maxillarpalpen (233, von oben, x300; 234, von unten, x260).

WEIBCHEN (Abb. D, E, H).

Ausserdem verweise ich auf die Gesamtaufnahme eines ♀ von Nelshoogte, E-Y:2350, Abb. D, E und die Basis des Halsschildes Abb. H.

EINGESEHENES MATERIAL: South Africa, Natal: Frere, ix. und x.1892, G. A. K. Marshall, 3 ♀ (BM), det. G. C. Champion; Weza, Impetyene grassveld, flowering grass, grass tussocks and intersept. trap 12 days, 30°37'S, 29°42'E, 16.-21.xi.1989, E-Y:2680, 2709, 2712, 2718, S. Endrödy-Younga, I. Klimaszewski, 8 Ex. (TMP), 5 Ex. (NHMB). Transkei: Fraser Gorge, grass tussocks, 31°24'S, 29°42'E, 27.xi.1988, E-Y:2584, S. Endrödy-Younga, 10 Ex. (TMP), 5 Ex. (NHMB). E Transvaal: Uitsoek Forest Station, 1100 m, grassveld, 12.xii.1986, 6.v.1987, E-Y:2379, 2426, 25°18'S, 30°55'E, S. Endrödy-Younga, 39 Ex. (TMP), 11 Ex. (NHMB); Gods Window, grassnetting, 24°35'S, 30°51'E, 12.xi.1980, E-Y:1734, S. Endrödy-Younga, 14 Ex. (TMP).

Die von Champion (1922) als *albilabris* bestimmten Exemplare aus Salisbury (jetzt Harare) (Zimbabwe) gehören einer neuen Art an, die ich hier als *majeri* Wittmer beschreibe.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

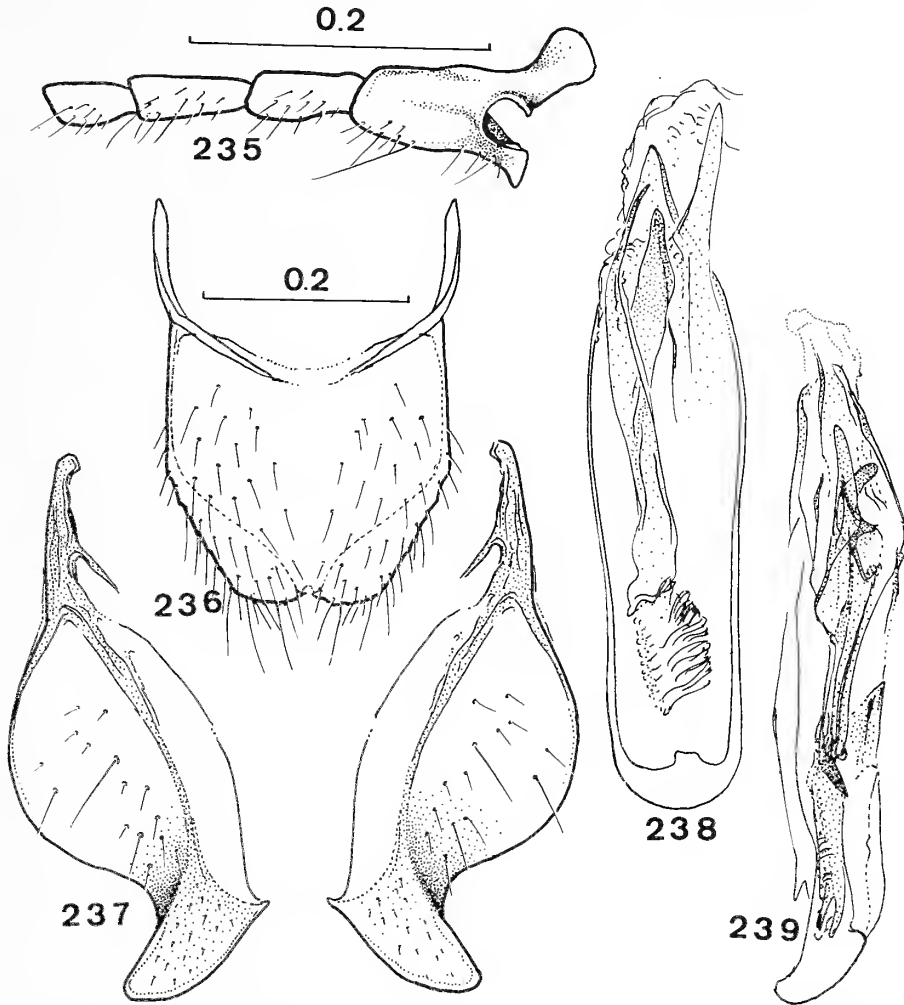


Abb. 235-239. *Sphinginopalpus* s. str. *albilabris* (Boheman) ♂: 235, Fühlerglieder 1-4; 236, Tergit 8; 237, Sternit 8; 238-239, Kopulationsapparat (238, dorsal; 239, Profil). Massstab von 235 auch für 237-239.

38. *Sphinginopalpus s. str. complexus* sp. nov.

MÄNNCHEN (Abb. 240-245).

Länge 2 mm.

Eine in Körperform und Färbung mit *albilabris* (Boheman) übereinstimmende Art. Sie unterscheidet sich durch die Form der Maxillarpalpen (Abb. 240-241), die zum grössten Teil gelb sind, nur Glied 1 ist teils leicht angedunkelt, Fühler Abb. 242, Tergit 8 Abb. 243, Sternit 8 Abb. 244, Kopulationsapparat Abb. 245 dorsal, vergleiche mit den Abbildungen 233-239.

Holotypus und 28 Paratypen (NHMB), 2 Paratypen (TMP), 2 Paratypen (AMG): South Africa, Transvaal: Bothasnek, 1450 m, 23.xi.1987, W. Wittmer.

Diese neue Art ist neben *albilabris* (Boheman) zu stellen, von der sie sich durch die verschiedenen Terminalia unterscheidet. Die Maxillarpalpen (Abb. 240-241) gleichen sehr *albilabris*.

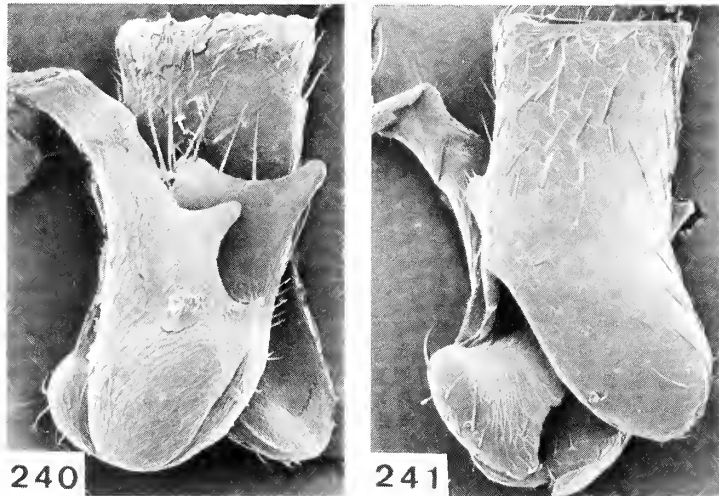


Abb. 240-241. *Sphinginopalpus s. str. complexus* sp. nov. ♂: 240-241, Maxillarpalpen (x250) (240, von oben; 241, von unten).

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

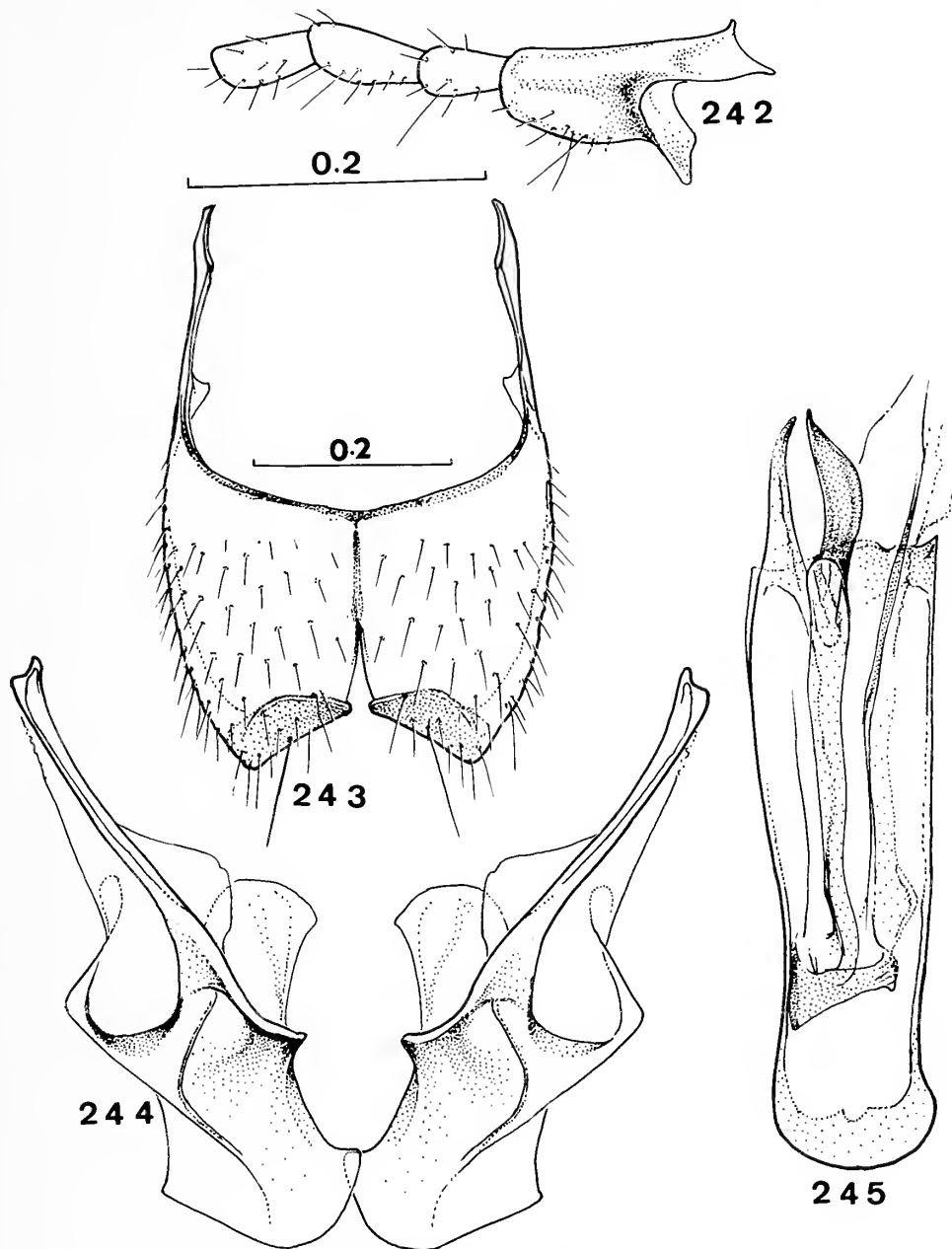


Abb. 242-245. *Sphinginopalpus* s. str. *complexus* sp. nov. ♂: 242, Fühlerglieder 1-4; 243, Tergit 8; 244, Sternit 8; 245, Kopulationsapparat (dorsal). Massstab von 242 auch für 244, 245.

39. *Sphinginopalpus* s. str. *politipennis* sp. nov.

MÄNNCHEN (Abb. 246-251).

Länge fast 2,5 mm.

Kopf schwarz, von der Mitte der Augen nach vorne, inklusive der Wangen, gelb; Maxillarpalpen schwarz; Fühler gelb, die letzten 4 bis 5 Glieder schwärzlich; Halsschild schwarz, ein Teil der abgesetzten Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere jederseits mit einem schmalen, kurzen, antemedianen weisslichen Flecken; Hinterschenkel schwarz, Hintertibien schwärzlich, an der Basis kurz aufgeheilt, Hintertarsen braun, 4 Vorderschenkel schwarz, an den Knien kurz heller, 4 vordere Schienen und Tarsen gelb.



Abb. 246-247. *Sphinginopalpus* s. str. *politipennis* sp. nov. ♂: 246-247, Maxillarpalpen (x170) (246, von oben; 247, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 246-247. Fühler (Abb. 248) um ca. 1/5 kürzer als die Flügeldecken, Zahn an Glied 1 mit sehr langer und schmaler Spitze, 3 nur wenig länger als 4. Halsschild länger als breit (15,5x14), sonst wie bei *oculimaculatus*, jedoch Chagrinierung an der abgeflachten Basis feiner. Flügeldecken langoval, die falschen Epipleuren konnten nicht gemessen werden, weil die Decken beidseitig eingerollt sind; Oberfläche glatt, Punktierung sehr spärlich. Tergit 8 Abb. 249. Sternit 8 Abb. 250.

Kopulationsapparat Abb. 251.

Holotypus (TMP), 1 Paratypus (NHMB): South Africa, E Transvaal: Nelshoogte, Devils Knuckle, grassnetting, 25°47'S, 30°49'E, 4.xii.1986, E-Y:2350, S. Endrödy-Younga.

Die stark glänzenden Flügeldecken mit den verhältnismässig wenig weit nach hinten reichenden Punkten, nebst den Terminalia, unterscheiden diese Art von den vielen ähnlich gefärbten.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

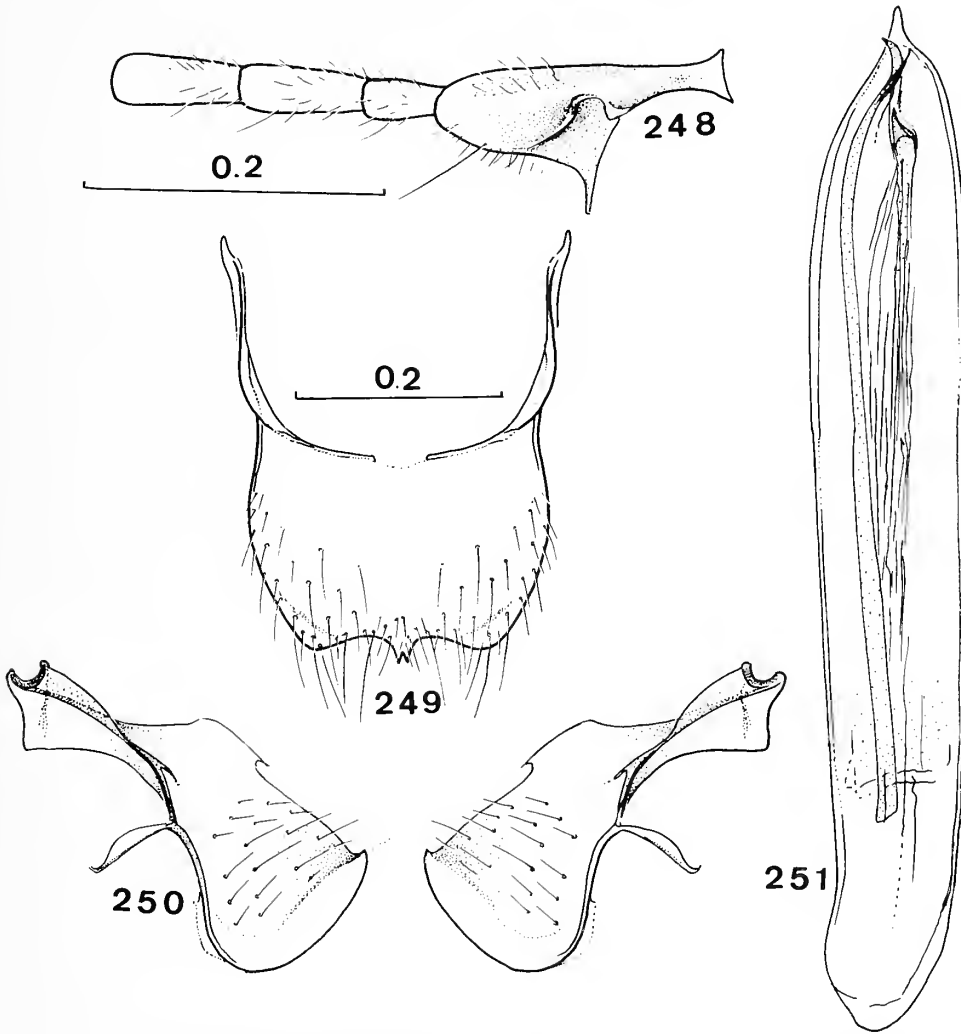


Abb. 248-251. *Sphinginopalpus* s. str. *politipennis* sp. nov. ♂: 248, Fühlerglieder 1-4; 249, Tergit 8; 250, Sternit 8; 251, Kopulationsapparat (dorsal). Massstab von 248 auch für 250, 251.

40. *Sphinginopalpus* s. str. *trispinopsis* sp. nov.

MÄNNCHEN (Abb. 252-255).

Länge 2,2 mm.

Eine in der Färbung und Körperform mit *trispinus* Wittmer übereinstimmende Art, nur bei den Fühlern fehlt der kleine schwarze Flecken auf Glied 3, dafür ist 4 bereits angedunkelt, bei *trispinus* gelb.

Fühler Abb. 252. Die Maxillarpalpen sind denen von *trispinus* sehr ähnlich und werden deshalb nicht abgebildet. Tergit 8 Abb. 253. Sternit 8 (Abb. 254) und der Kopulationsapparat (Abb. 255) zeigen grössere Unterschiede.

WEIBCHEN.

Fühlerglieder 1 bis 5 gelb, nur 1 an der Basis ganz wenig dunkel, sonst wie das ♂ gefärbt; ungeflügelt.

Holotypus ♂ und 1 Paratypus ♀ (TMP), 1 Paratypus ♀ (NHMB): South Africa, E Transvaal: Gods Window, grassnetting, 24°35'S, 30°51'E, 12.xi.1980, E-Y:1734, S. Endrödy-Younga.

Diese neue Art gehört zu einer kleinen Gruppe deren Fühlerglied 1 mit drei Zähnen bewehrt ist (*tridens*, *tridensmimus*).

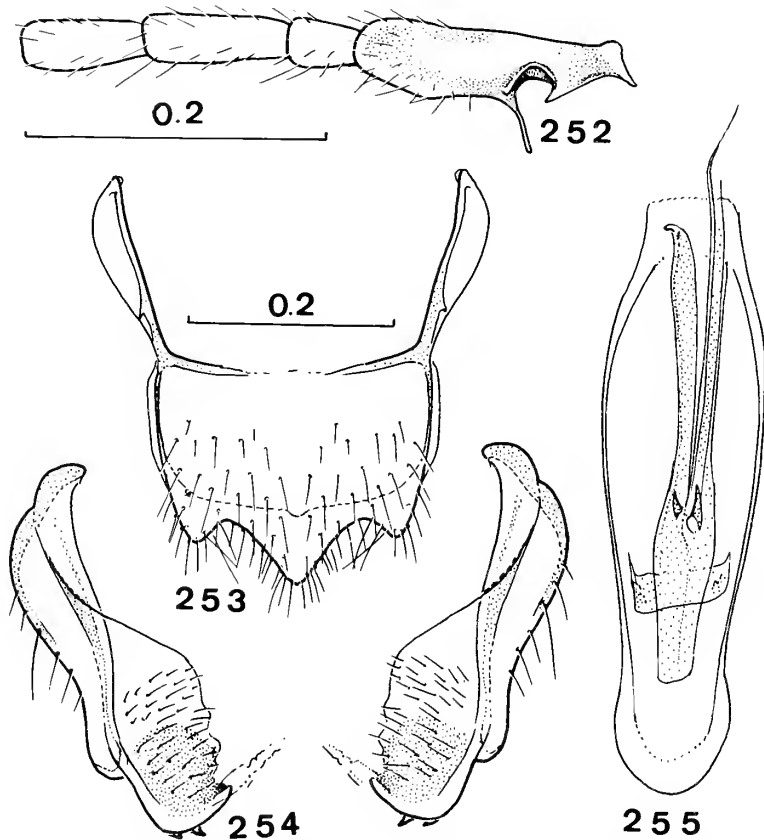


Abb. 252-255. *Sphinginopalpus* s. str. *trispinopsis* sp. nov. ♂: 252, Fühlerglieder 1-4; 253, Tergit 8; 254, Sternit 8; 255, Kopulationsapparat (dorsal). Massstab von 252 auch für 254, 255.

41. *Sphinginopalpus* s. str. *oneili* Pic.

Sphinginopalpus oneili Pic, 1903: 164. - 1904: 13. - Champion, 1922: 328, T. 5, Fig. 21, *parte*.

MÄNNCHEN (Abb. 256-264).

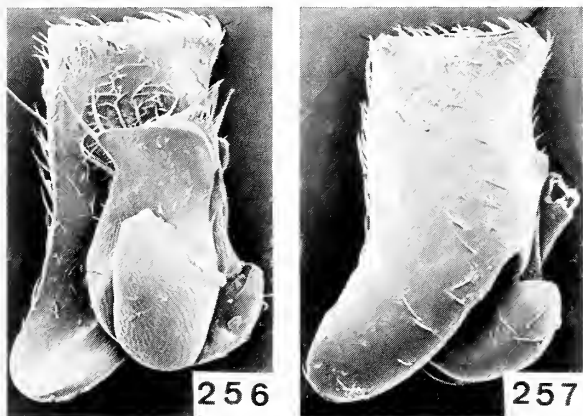


Abb. 256-257. *Sphinginopalpus* s. str. *oneili* Pic ♂: 256-257, Maxillarpalpen (x155) (256, von oben; 257, von unten).

Im MP befindet sich der Lectotypus und 7 Paralectotypen, im BM 4 Paralectotypen, im SAM 3 Paralectotypen, im NHMB 1 Paralectotypus. Originalfundort: Dunbrody (Cape Prov.), 33°28'S, 25°33'E. Für die verschiedenen Abbildungen diente der Lectotypus. Maxillarpalpen Abb. 256-257. Fühler Abb. 258. Tergit 8 Abb. 259. Sternit 8 Abb. 260. Spiculum Abb. 261. Tegmen Abb. 262.

Kopulationsapparat Abb. 263 dorsal, Abb. 264 Profil.

WEIBCHEN (Abb. 265).

Champion (1922) stellte eine Anzahl von Exemplaren von Salisbury (jetzt Harare) (Zimbabwe) zu *oneili*, die einer anderen, neuen Art angehören, die ich hier als *majeri* Wittmer beschreibe.

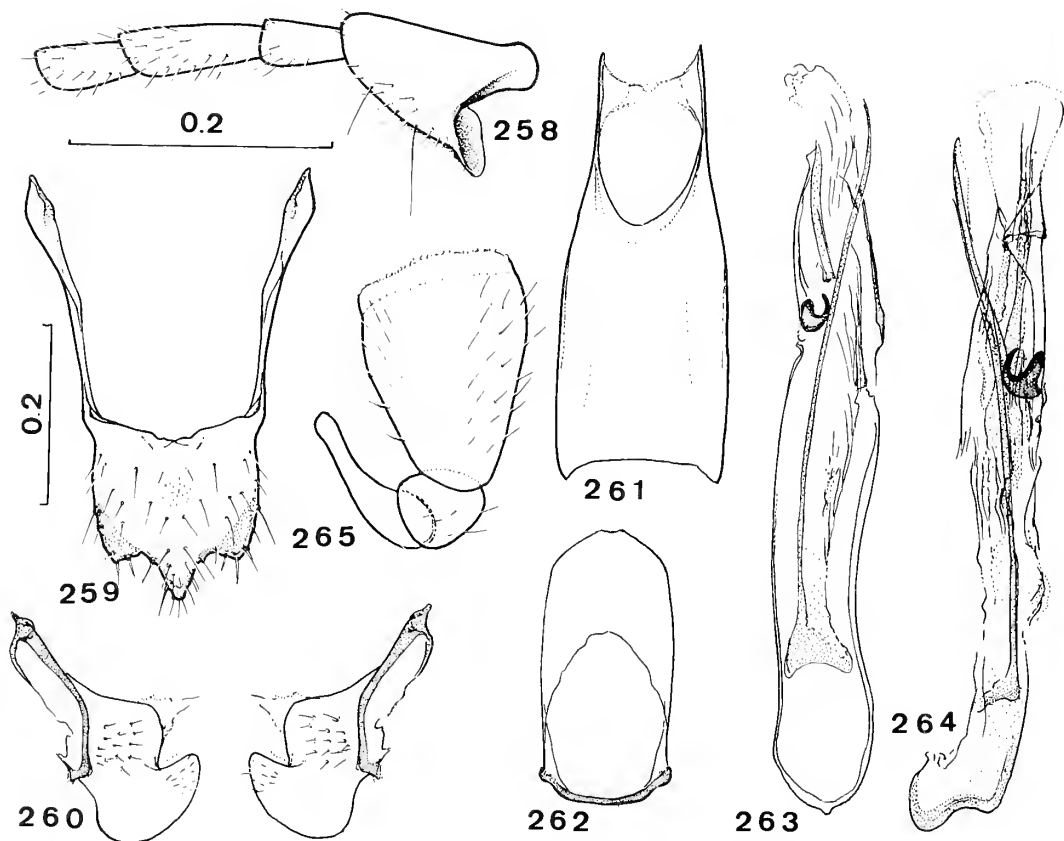


Abb. 258-265. *Sphinginopalpus* s. str. *oneili* Pic ♂: 258, Fühlerglieder 1-4; 259, Tergit 8; 260, Sternit 8; 261, Spiculum; 262, Tegmen; 263-264, Kopulationsapparat (263, dorsal; 264, Profil); 265, *Sphinginopalpus* s. str. *oneili* Pic ♀: Maxillarpalpus. Massstab von 258 auch für 265 und 259 auch für 261-264.

42. *Sphinginopalpus* s. str. *leucosideae* sp. nov.

MÄNNCHEN (Abb. 266-271).

Länge 2 mm.

Kopf schwarz, ein gelber Flecken auf dem Vorderkopf, zwischen den Fühlerwurzeln, die Augen und Wangen nicht erreichend; Maxillarpalpen schwarzbraun, teils schwach aufgehellt; Fühler dunkel, die Glieder 1 bis 5 gelb, Basis von 1 schwarz und mit einem schwarzen Längswisch auf der Oberseite; Halsschild schwarz, die ganze abgeflachte Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem weisslichen, antimedialen, dreieckigen Seitenflecken, der sich etwas mehr nach hinten als nach vorne hinzieht, die Naht wird nicht erreicht; Hinterbeine schwarz, Hintertarsen leicht aufgehellt, 4 vordere Schenkel schwarz, 4 vordere Tibien und Tarsen gelb.

Kopf mit den Augen ein wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt.

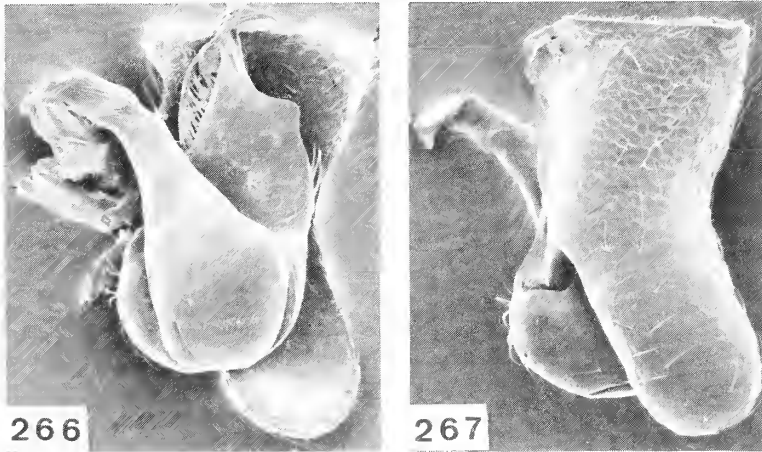


Abb. 266-267. *Sphinginopalpus* s. str. *leucosideae* sp. nov. ♂: 266-267, Maxillarpalpen (x170) (266, von oben; 267, von unten).

Maxillarpalpen Abb. 266-267. Fühler (Abb. 268) um fast 1/4 kürzer als die Flügeldecken, Glied 3 ein wenig länger als 4. Halsschild länger als breit (18x15), Oberfläche glatt, abgeflachter Teil chagriniert, sonst wie *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, nicht krenuliert; Punkte grob, in Reihen angeordnet, nach der Mitte wenig tief, verworren, spärlicher und fast ganz erlöschend. Tergit 8 Abb. 269. Sternit 8 Abb. 270.

Kopulationsapparat Abb. 271 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz; Fühlerglied 1 gelb, nur die Basis kurz schwarz, Schulterbeulen stark ruduziert, wahrscheinlich ungeflügelt.

Holotypus (NMB): South Africa, Orange Free State: Golden Gate Highlands National Park, SE 28 28 BC, 13.-14.xi.1985, ex *Leucosidea sericea*, Mus. staff. Natal: Nyala Reserve, 10 km inland of Empangeni, in *Acacia* veld, 10.ii.1985, P. E. Reavell, 1 Paratypus (NHMB); Ukulu River, swept in grass, flood plain, P. E. Reavell, 1 Paratypus (NHMB); 4 km S Wasbank, R 621, 1030 m, 21.xi.1987, W. Wittmer, 4 Paratypen (NHMB).

Diese neue Art scheint weit verbreitet zu sein, sie ist leicht erkennbar an dem ziemlich parallelen Fühlerglied 1 sowie an den Terminalia.

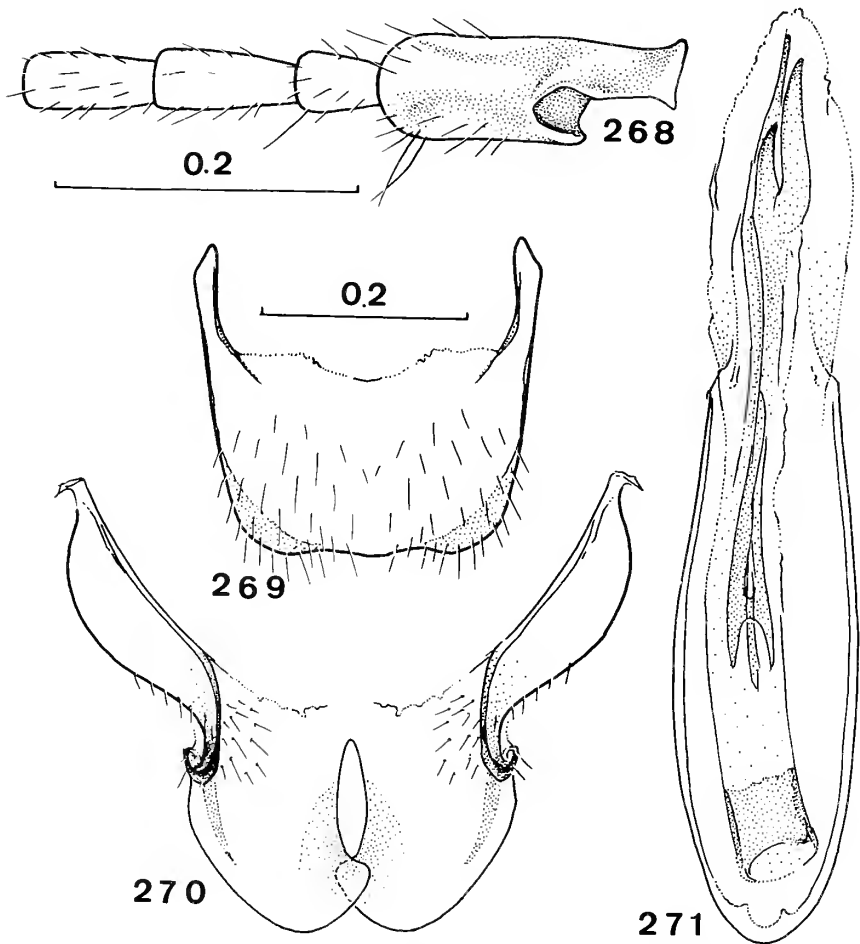


Abb. 268-271. *Sphinginopalpus* s. str. *leucosideae* sp. nov. ♂: 268, Fühlerglieder 1-4; 269, Tergit 8; 270, Sternit 8; 271, Kopulationsapparat (dorsal). Massstab von 268 auch für 270-271.

43. *Sphinginopalpus* s. str. *amatolensis* sp. nov.

MÄNNCHEN (Abb. 272-277).

Länge 2,5 mm.

Kopf mit den Wangen schwarz, zwischen den Fühlerwurzeln gelb und einem kleinen gelblichen Flecken neben jedem Auge, der auch fehlen kann; Maxillarpalpen schwärzlich, Glied 1 aufgeheilt; Fühler schwarz, Glieder 1 bis 5 gelb, Oberseite von 1 schwarz; Halsschild schwarz, abgeflachte Basis schmal gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem weisslichen, antimedianen Querband, das an der Naht unterbrochen und seitlich verlängert ist; Hinterbeine

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schwarz, Tarsen teils aufgeheilt, 4 Vorderbeine schwarz bis schwärzlich, 4 Vordertarsen gelb.

Kopf mit den Augen ein wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 272-273. Fühler (Abb. 274) um nicht ganz 1/5 kürzer als die Flügeldecken, Glied 1 mit sehr kleinem, feinem Zahn, 3 kaum merklich länger als 4. Halsschild länger als breit (18x16), aufgewölbter Teil weniger stark chagriniert als der Kopf, abgeflachter Teil chagriniert, sonst wie *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, ganz schwach krenuliert; Punktierung ähnlich wie bei *elongatidens*. Tergit 8 Abb. 275. Sternit 8 Abb. 276.

Kopulationsapparat Abb. 277 dorsal.

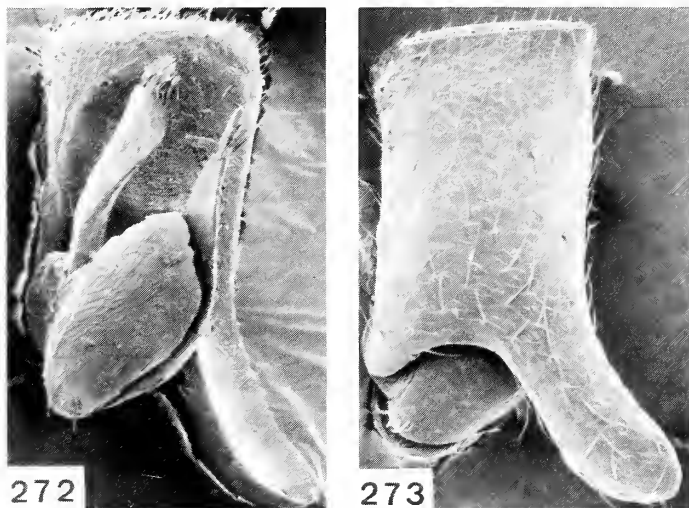


Abb. 272-273. *Sphinginopalpus* s. str. *amatolensis* sp. nov. ♂: 272-273, Maxillarpalpen (x170) (272, von oben; 273, von unten).

WEIBCHEN.

Kopf einfarbig schwarz, sonst wie das ♂ gefärbt. Schulterbeulen nur angedeutet; falsche Epipleuren fein krenuliert; ungeflügelt.

Holotypus und 20 Paratypen (TMP), 10 Paratypen (NHMB), 2 Paratypen (AMG): South Africa, Cape Prov.: Amatole, Isidenge Forest Station, grass tussocks, 32°41'S, 27°15'E, 18.xi.1987, E-Y:2524, S. Endrödy-Younga. Natal: Mouth of Umkomaas River, ix.1897, G. A. K. Marshall, 1 Paratypus (BM), von Champion als *myrmecodes/albifrons* bestimmt.

Diese neue Art ist neben *trimaculatus* Wittmer zu stellen. Die von Champion (1922) als *myrmecodes* Boheman bestimmten und beschriebenen ♂ ♀ mit Fundorten "mouth of Umkomaas River" und Seymour" gehören zu *amatolensis*.

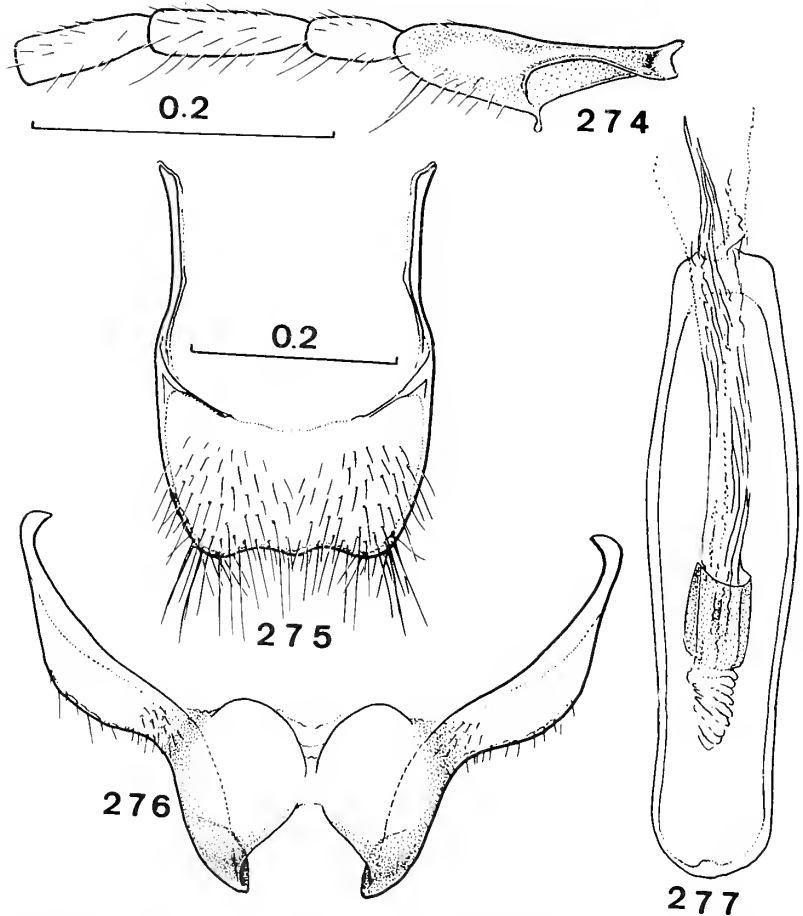


Abb. 274-277. *Sphinginopalpus* s. str. *amatolensis* sp. nov. ♂: 274, Fühlerglieder 1-4; 275, Tergit 8; 276, Sternit 8; 277, Kopulationsapparat (dorsal). Massstab von 274 auch für 276, 277.

44. *Sphinginopalpus* s. str. *nelshoogtensis* sp. nov.

MÄNNCHEN (Abb. 278-283).

Länge 2,8 mm.

Kopf mit den Wangen schwarz, neben jedem Auge ein ganz kleiner, verschwommener heller Flecken; Maxillarpalpen schwärzlich; Fühler dunkel. Glied 1 auf der Unterseite und 2 bis 5 ganz hell; Halsschild schwarz, Basis nicht ganz bis zur Hälfte der abgeflachten Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem gelblichweissen, antimedialen Querband, das an der Naht unterbrochen ist, seitlich beidseitig ein wenig verlängert; die 4 hinteren Beine schwarz, Tarsen schwach aufgehellt, Vorderbeine dunkel, Schenkel gegen das Knie und Tarsen aufgehellt.

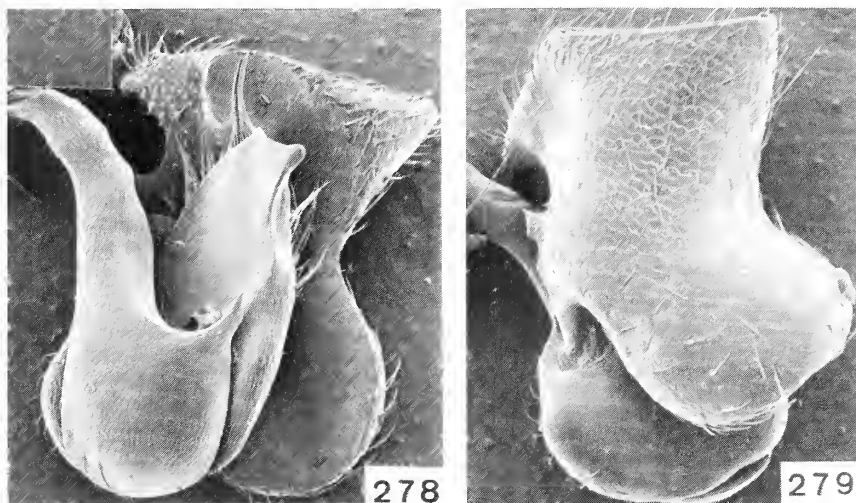


Abb. 278-279. *Sphinginopalpus* s. str. *nelshoogtensis* sp. nov. ♂ : 278-279, Maxillarpalpen (x200) (278, von oben; 279, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 278-279, Fühler (Abb. 280) um ca. 1/5 kürzer als die Flügeldecken, Glied 3 deutlich länger als 4. Halsschild breiter als lang (20x15,5), sonst wie bei *majeri*; auf dem abgeflachten Teil jederseits neben dem Seitenrand eine feine Längsrippe (bei *majeri* nicht mit Sicherheit erkennbar). Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, keine Krenulierung; Punktreihen besonders in der Mitte regelmässig, an der Basis und hinter der Mitte Punkte verworren, gegen die Spitze immer mehr erlöschend. Tergit 8 Abb. 281. Sternit 8 Abb. 282.

Kopulationsapparat Abb. 283 dorsal.

Holotypus (TMP): South Africa, E Transvaal: Nelshoogte, grassnetting, 25°47'S, 30°49'E, 8.iv.1987, E-Y:2456, S. Endrödy- Younga.

Diese neue Art ist leicht an der Färbung des Kopfes und der Flügeldecken zu erkennen, bei letzteren reicht das antimediane, helle Querband bis fast zur Naht. Das Fühlerglied 1 hat einen breiten, stumpfen Zahn.

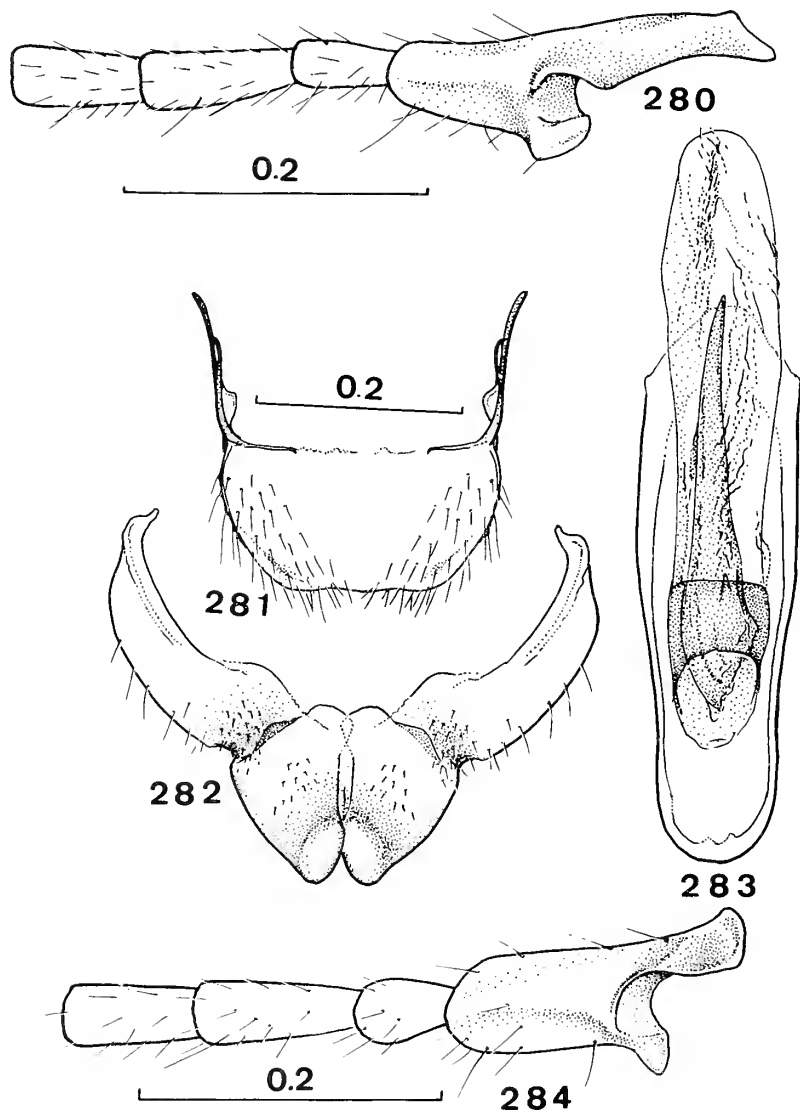


Abb. 280-284. 280-283. *Sphinginopalpus* s. str. *nelshoogtensis* sp. nov. ♂: 280, Fühlerglieder 1-4; 281, Tergit 8; 282, Sternit 8; 283, Kopulationsapparat (dorsal). Massstab von 280 auch für 282, 283. 284. *Sphinginopalpus* s. str. *nelshoogtensis transformatus* ssp. nov. ♂: Fühlerglieder 1-4.

45. *Sphinginopalpus* s. str. *nelshoogtensis transformatus* ssp. nov.

MÄNNCHEN (Abb. 284).

Länge 2,3 mm.

Wie die Nominatform gefärbt, nur der Flecken neben jedem Auge ist grösser, er zieht sich schmal gegen die Fühlerwurzeln und um diese herum, seitlich auch ein wenig auf die Wangen; das Fühlerglied 1 ist nur an der Basis kurz und schwach dunkler und die Maxillarpalpen sind gelb anstatt schwärzlich.

Die Maxillarpalpen sind ähnlich gebaut wie bei der Nominatform, doch bei den Fühlern (Abb. 284) ist das Glied 1 sehr verschieden. Aufgrund dieser Merkmale könnte man *transformatus* wohl als eigene Art anerkennen, wenn die Terminalia und der Kopulationsapparat nicht so ausserordentlich ähnlich wären. Deshalb möchte ich *transformatus* nur als Unterart von *nelshoogtensis* beschreiben.

Holotypus (NHMB): South Africa, Natal: Manguzi Forest, Kosi, 26°58'S, 32°44'E, 10.i.1985, edge of swamp forest, P. E. Reavell.

46. *Sphinginopalpus* s. str. *quadratipalpus* sp. nov.

MÄNNCHEN (Abb. 285-290).

Länge 2,3-2,4 mm.

Kopf schwarz mit 3 gelben Flecken, je einem kleinen neben den Augen und einem grossen am Vorderkopf, die Wangen nicht einschliessend, oder Flecken neben den Augen fehlen (Fundort E-Y:2584); Maxillarpalpen letztes Glied schwärzlich, vorletztes teilweise stark gelblich aufgehell; Fühlerglieder 1 bis 4, oder 1 bis 6-7 gelb, Oberseite von 1 schwarz und die letzten dunkel; Halsschild schwarz, Basis mehr oder weniger breit gelbbraun; Schildchen und Flügeldecken schwarz, letztere

mit einem breiten, weisslichen, antimedialen Querband, das an der Naht unterbrochen ist, an den Seiten verbreitert; Hinterbeine schwarz, oder die Hintertarsen schwach aufgehell, 4 vordere Tarsen gelb, 4 Vorderbeine schwarz, Tibien an der Basis und Spitze der Schenkel etwas aufgehell.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 285-286. Fühler (Abb. 287) um ca. 1/4 kürzer als die Flügeldecken, Glied 3 deutlich länger als 4.



Abb. 285-286. *Sphinginopalpus* s. str. *quadratipalpus* sp. nov. ♂: 285-286, Maxillarpalpen (x200) (285, von oben; 286, von unten).

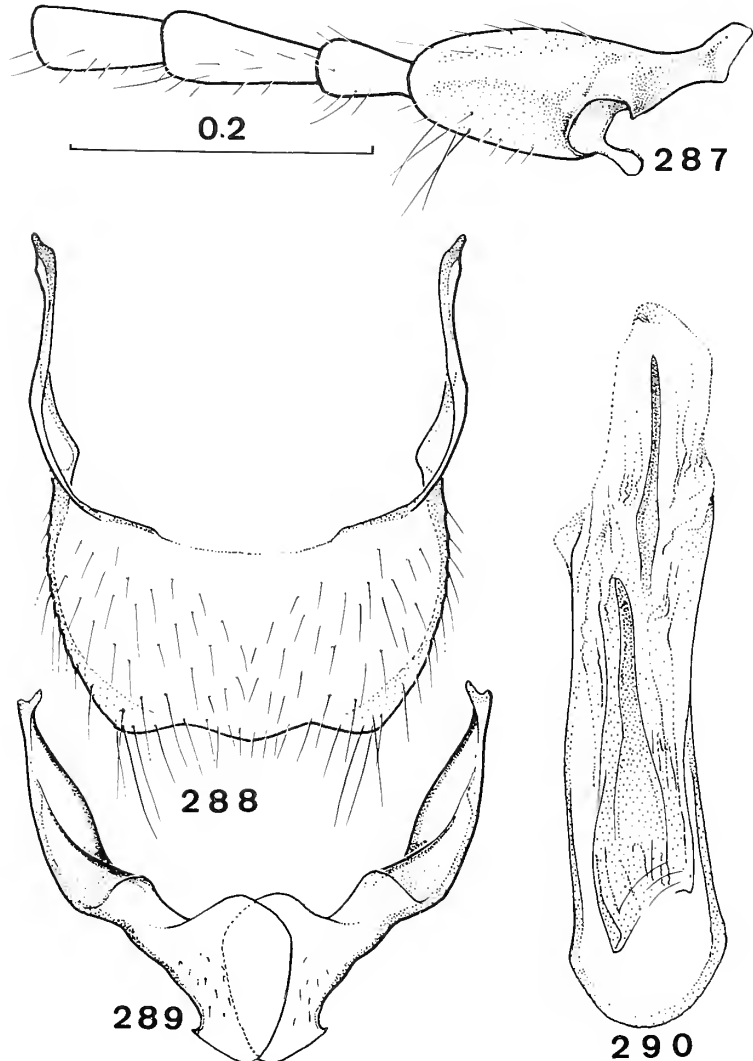


Abb. 287-290. *Sphinginopalpus* s. str. *quadratipalpus* sp. nov. ♂: 287 Fühlerglieder 1-4; 288, Tergit 8; 289, Sternit 8; 290, Kopulationsapparat (dorsal). Massstab gilt für 287-290.

Halsschild länger als breit (18x15,5), Seiten von der Mitte nach vorne fast gerade, kaum merklich gerundet, leicht verengt; aufgewölbter Teil glatt, abgeflachter Teil chagriniert. Flügeldecken langoval, falsche Epipleuren ca. 60% der Länge einnehmend, Krenulierung nur angedeutet, kaum sichtbar; Punkte grob, bis zur Mitte und zum Teil darüber hinaus in Reihen angeordnet, Punkte nach hinten mehr erlöschend. Tergit 8 Abb. 288. Sternit 8 Abb. 289.

Kopulationsapparat Abb. 290 dorsal.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

Holotypus (TMP): South Africa, Transkei: Fraser Gorge, grass tussocks, 31°24'S, 29°42'E, 27.xi.1988, E-Y:2584, S. Endrödy-Younga. Natal Middl.: Karkloof, grassveld, 29°19'S, 30°15'E, 10.xii.1989, E-Y:2758, S. Endrödy-Younga, 1 Paratypus (NHMB).

Eine durch die Form der Maxillarpalpen charakterisierte Art, deren Glied 3 distal fast quadratisch ist; auch bei dieser Art ist das helle, antimediane Querband erst kurz vor der Naht unterbrochen. Weitere Unterschiede zeigt der Bau von Fühlerglied 1 und die Terminalia.

47. *Sphinginopalpus* s. str. *trimaculatus* sp. nov.

MÄNNCHEN (Abb. 291-297).

Länge 2,3-2,5 mm.

Kopf schwarz mit 3 gelben Flecken, der grösste am Vorderkopf und je ein weiterer neben jedem Auge, diese beiden manchmal nur angedeutet, Wangen schwarz, der Flecken am Vorderkopf manchmal stark reduziert, sodass nur ein schmales gelbes Band ganz vorne verbleibt; Maxillarpalpen vorwiegend schwarz; Fühlerglieder 1 bis 5 gelb, oft auch 6 teilweise, 7 bis 11 und Oberseite von 1, dieses teilweise, schwarz; Halsschild schwarz, abgeflachte Basis grösstenteils gelbbraun; Schildchen und Flügeldecken schwarz, letztere jederseits vor der Mitte mit einem weisslichen, fast dreieckigen Flecken, der die Naht nicht erreicht; Beine schwarz, die vier vorderen ein wenig aufgehellt, die 4 vorderen Tarsen stärker aufgehellt.

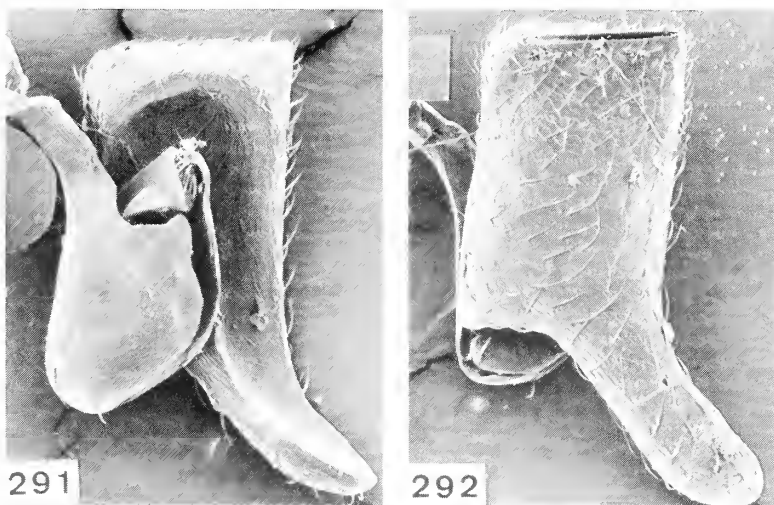


Abb. 291-292. *Sphinginopalpus* s. str. *trimaculatus* sp. nov. ♂: 291-292, Maxillarpalpen (x170) (291, von oben; 292, von unten).

Kopf mit den Augen praktisch so breit wie der Halsschild, Stirne leicht gewölbt; Oberfläche feinstens chagriniert. Maxillarpalpen Abb. 291-292. Fühler (Abb. 293) um ca. 1/5 kürzer als die Flügeldecken, Glied 1 beidseitig schwach, fast regelmässig gerundet, Zahn klein, schmal, 3 und 4

parallel, 3 deutlich länger als 4. Halsschild länger als breit (20x17), wie *capensis* gebaut; Oberfläche auf der Scheibe glatt, an den Seiten und abgeflachte Basis chagriniert, einzelne Punkte, zum Teil ziemlich stark erloschen, vorhanden. Flügeldecken langoval, sonst wie bei *capensis*, aber stärker punktiert, falsche Epipleuren ca. 60% der Länge einnehmend, Krenulierung sehr fein, nur angedeutet; lange aufstehende Haare vereinzelt, Tergit 8 Abb. 294. Sternit 8 Abb. 295.

Kopulationsapparat Abb. 296 dorsal, Abb. 297 Innensack leicht verschoben.

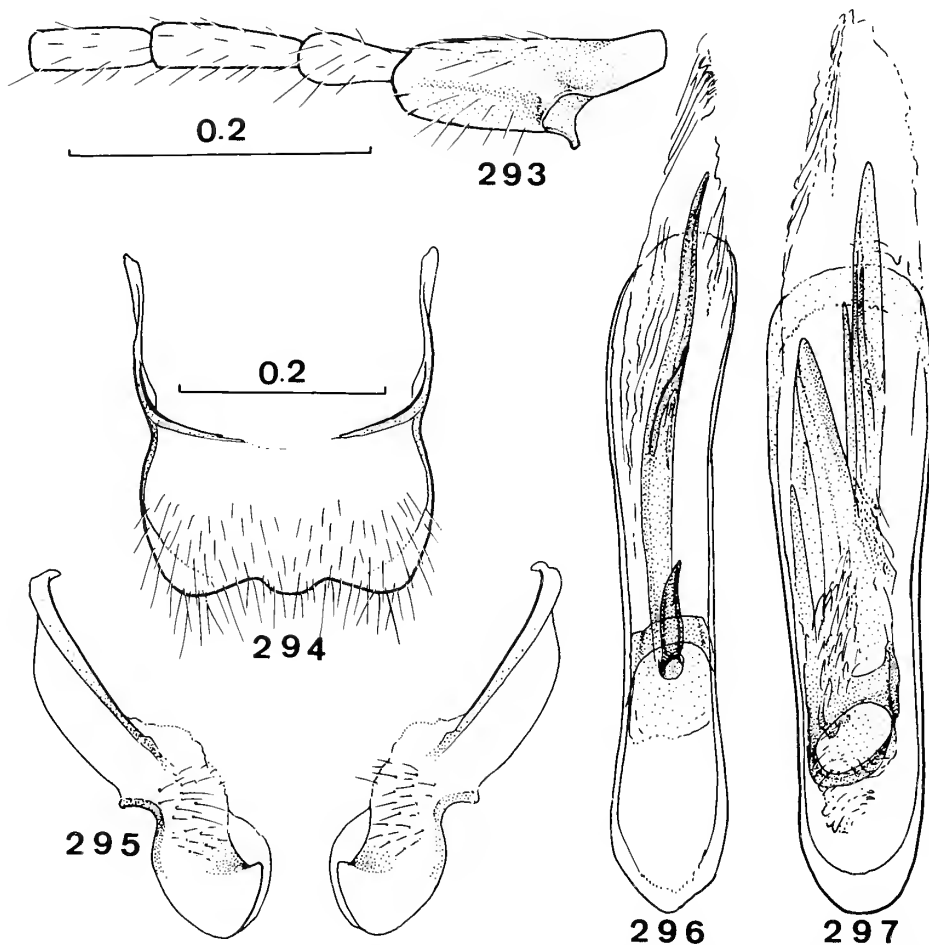


Abb. 293-297. *Sphinginopalpus* s. str. *trimaculatus* sp. nov. ♂: 293, Fühlerglieder 1-4; 294, Tergit 8; 295, Sternit 8; 296-297, Kopulationsapparat (296, dorsal; 297, mit leicht verschobenem Innensack). Massstab von 293 auch für 295-297.

WEIBCHEN.

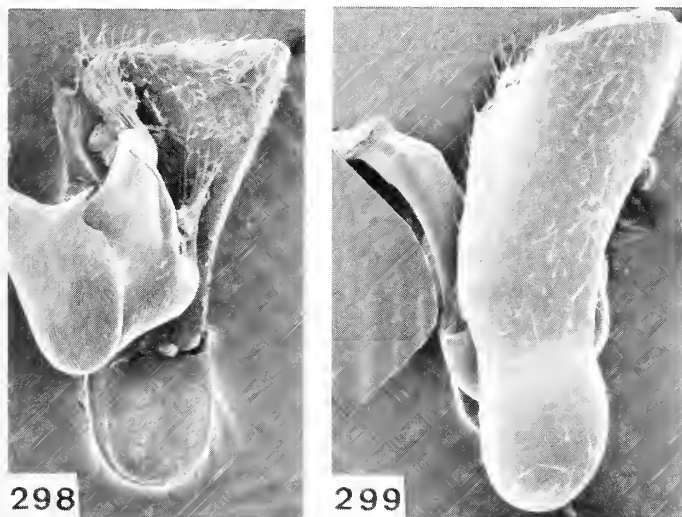
Kopf einfarbig schwarz, sonst wie das ♂ gefärbt. Schulterbeulen stark zurückgebildet, gerundet; Krenulierung der falschen Epipleuren wie beim ♂.

Holotypus und 5 Paratypen (TMP), 5 Paratypen (NHMB), 2 Paratypen (AMG): South Africa, Natal: Weza, Impetyene, grassveld, intersept. trap, 30°37'S, 29°42'E, 16.xi.1989, E-Y:2680, S. Endrödy-Younga, I. Klimaszewski; Bergville Distr., Indumeni for., humus, x.1960, N. Leleup, 1 Paratypus (TMP); Karkloof grassveld, 29°19'S, 30°15'E, 7.xii.1989, E-Y:2747, 2756, 2758, S. Endrödy-Younga, 2 Paratypen (TMP), 1 Paratypus (NHMB); Cathedral Peak, Drakensberg, 6.xi.1981, J. & S. Klapperich, 3 Paratypen (NHMB). E Transvaal: Uitsoek, high altitude grassveld, 25°15'S, 30°34'E, 6.ii.1987, E-Y:2426, S. Endrödy-Younga, 2 Paratypen (TMP), 1 Paratypus (NHMB); Berlin, gorge edge, 24°32'S, 30°44'E, 4.ii.1987, E-Y:2413, S. Endrödy-Younga, 2 Paratypen (TMP); Nelshoogte Forest Station, 25°47'S, 30°50'E, 4.xii. 1987, E-Y:2336, 2340, 2350, 2456, S. Endrödy-Younga, 6 Paratypen (TMP), 3 Paratypen (NHMB). Transkei: Dwesa coast, grassland, 32°17'S, 28°51'E, 28.ii.1985, E-Y:2175, S. Endrödy-Younga, 1 Paratypus (TMP). E Cape Prov.: Katberg, 4000 ft, x.1932, R. E. Turner, 1 Paratypus (BM).

Eine hübsche kleine Art mit 3 hellen, kleinen Flecken auf dem Vorderkopf, sonst verweise ich auf die verschiedenen Abbildungen.

48. *Sphinginopalpus* s. str. *tridensmimus* sp. nov.

MÄNNCHEN (Abb. 298-303).



Länge 2,3-2,5 mm.

Kopf schwarz, Vorderkopf mit einer gelben Makel, die die Wangen nicht erreicht, neben jedem Auge eine kleine gelbe Makel; Maxillarpalpen schwarz; Fühler schwarz, erste 4 Glieder und Basis von 5 gelb, 1 an der Basis kurz dunkel; Halsschild schwarz, Basis schmal leicht aufgeheilt; Schildchen und Flügeldecken schwarz, letztere mit einem schwachen, seitlichen, antimedialen Saum, der nur die erste Punktreihe erreicht; Beine schwarz.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt.

Abb. 298-299. *Sphinginopalpus* s. str. *tridensmimus* sp. nov. ♂: 298-299, Maxillarpalpen (x170) (298, von oben; 299, von unten).

Maxillarpalpen Abb. 298-299. Fühler (Abb. 300) um ca. 1/5 kürzer als die Flügeldecken, Glied 1 mit 3 Zähnen, von denen der eine, obere, gegenüber dem basalen, bei der Ansicht von vorne nicht, oder kaum sichtbar ist (siehe Abbildung), von oben gesehen, ist ein kleiner stumpfer Zahn sichtbar, 3 deutlich länger als 4. Halsschild länger als breit (19x16); Seiten von der Mitte nach vorne praktisch parallel; Oberfläche glatt, nur an den Seiten des abgeflachten Teils fein chagriniert. Flügeldecken langoval; falsche Epipleuren ca. 60% der Länge einnehmend, Krenulierung nur angedeutet;

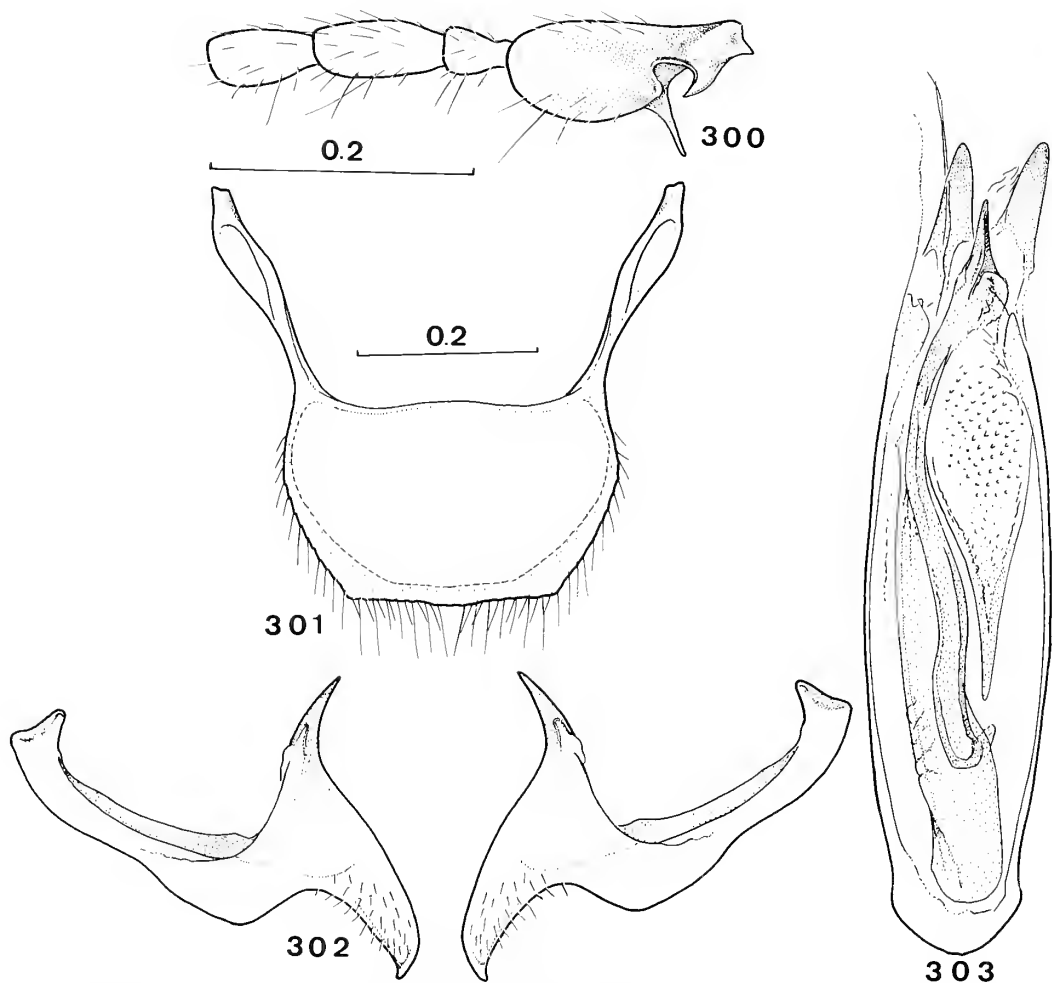


Abb. 300-303. *Sphinginopalpus* s. str. *tridensminus* sp. nov. ♂: 300, Fühlerglieder 1-4; 301, Tergit 8; 302, Sternit 8; 303, Kopulationsapparat (dorsal). Massstab von 300 auch für 302, 303.

Punktreihen bis zur Mitte deutlich, Punkte dann weiter auseinander stehend, weniger tief. Tergit 8 Abb. 301. Sternit 8 Abb. 302.

Kopulationsapparat Abb. 303 dorsal.

Holotypus (NHMB): South Africa, Natal: Golden Gate Park, Drakensberg, 6.xi.1981, J. & S. Klapperich.

Der Bau von Fühlerglied 1 erinnert an *tridens* Wittmer und die glatten Flügeldecken an *poliitipennis* Wittmer, doch sind letztere bei der neuen Art ein wenig stärker und dichter punktiert. Weitere Unterschiede liefern die Terminalia und der Kopulationsapparat.

49. *Sphinginopalpus* s. str. *longidens* Champion

Sphinginopalpus longidens Champion, 1922: 329.

MÄNNCHEN (Abb. 304-310).

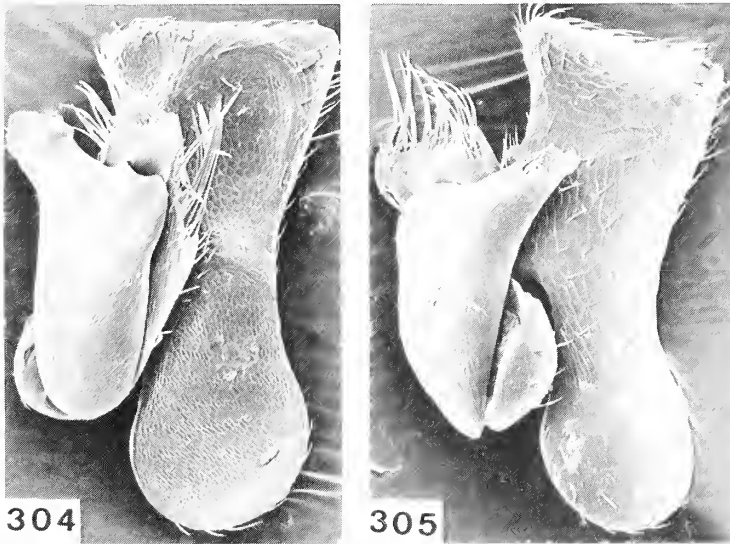


Abb. 304-305. *Sphinginopalpus* s. str. *longidens* Champion ♂: 304-305, Maxillarpalpen (x220) (304, von oben; 305, von unten).

Im BM befinden sich der Lectotypus und 7 Paralectotypen, im SAM 4 Paralectotypen.

Für die Abbildungen wurde der Lectotypus verwendet: Maxillarpalpen Abb. 304-305. Fühlerglieder 1 bis 4 (Abb. 306). Champion gibt in seiner Beschreibung an, dass das Glied 3 länger ist als 4, erwähnt aber nicht, dass es auch ein wenig breiter ist als 2 und 4. Tergit 8 Abb. 307. Sternit 8 Abb. 308. Kopulationsapparat Abb. 309 dorsal, Abb. 310 Profil.

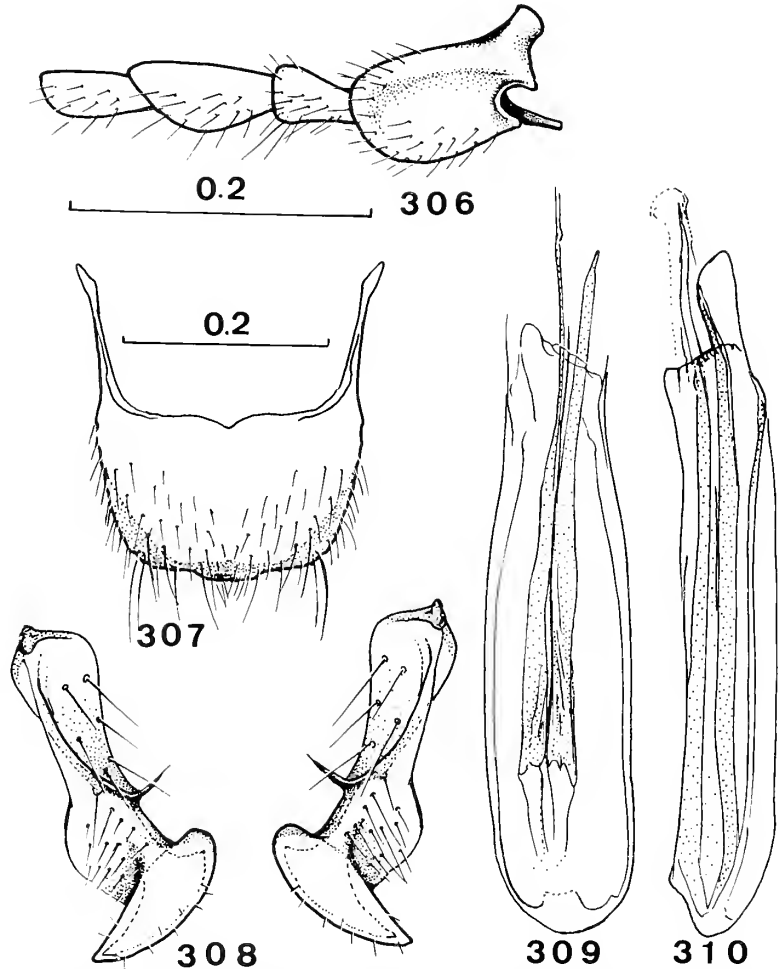


Abb. 306-310. *Sphinginopalpus* s. str. *longidens* Champion ♂: 306, Fühlerglieder 1-4; 307, Tergit 8, 308, Sternit 8; 309-310, Kopulationsapparat (309, dorsal; 310, Profil). Massstab von 306 auch für 308-310.

50. *Sphinginopalpus* s. str. *bidens* Champion

Sphinginopalpus bidens Champion, 1922: 328, T. 5, figs 20, 20a.

MÄNNCHEN (Abb. 311-317).

Der Holotypus befindet sich im BM, er stammt aus Frere (Natal) und diente zur Anfertigung folgender Abbildungen: Maxillarpalpen Abb. 311-312. Fühlerglieder 1 bis 4 Abb. 313. Tergit 8 Abb. 314. Sternit 8 Abb. 315. Kopulationsapparat Abb. 316 dorsal, Abb. 317 Profil.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

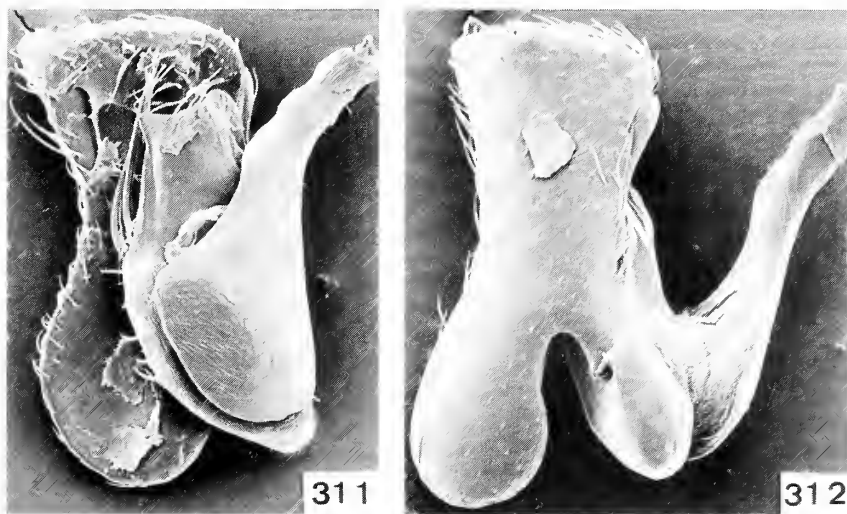


Abb. 311-312. *Sphinginopalpus* s.str. *bidens* Champion ♂: 311-312, Maxillarpalpen (x220) (311, von oben; 312, von unten).

EINGESEHENES MATERIAL: Transvaal: Pretoria, 20.xi.1981, J. & S. Klapperich, 1 ♂ (NHMB); Blydepoort, 20.xi.1981, J. & S. Klapperich, 3 ♂ (NHMB); 21/22 km S Lydenburg, 15.xi.1983, W. Wittmer, 1 ♂ (NHMB); Irene, 20.ii.1989, van Viegen (TMP); Middelburg, Cycas Farm, grassnetting, 25°31'S, 29°16'E, 5.xi.1985, E-Y:2262, S. Endrödy- Younga, 2 ♂ (TMP), 1 ♂ (NHMB). Transkei: S coast Dwesa Forest Station, 32°17'S, 28°50'E, 16.xii.1979, 26.ii.1985, E-Y:1687, 2168, S. Endrödy-Younga, 3 ♂ ♀ (TMP), 1 ♂ ♀ (NHMB).

Die gelblichweissen seitlichen Längsbänder sind beim Holotypus hinter den Schultern nur wenig erweitert. Bei den Exemplaren von den verschiedenen Fundorten finden sich solche mit dem hellen Seitensaum, währenddem die Flecken stark gegen die Naht erweitert sind.

WEIBCHEN.

Kopf einfarbig schwarz.

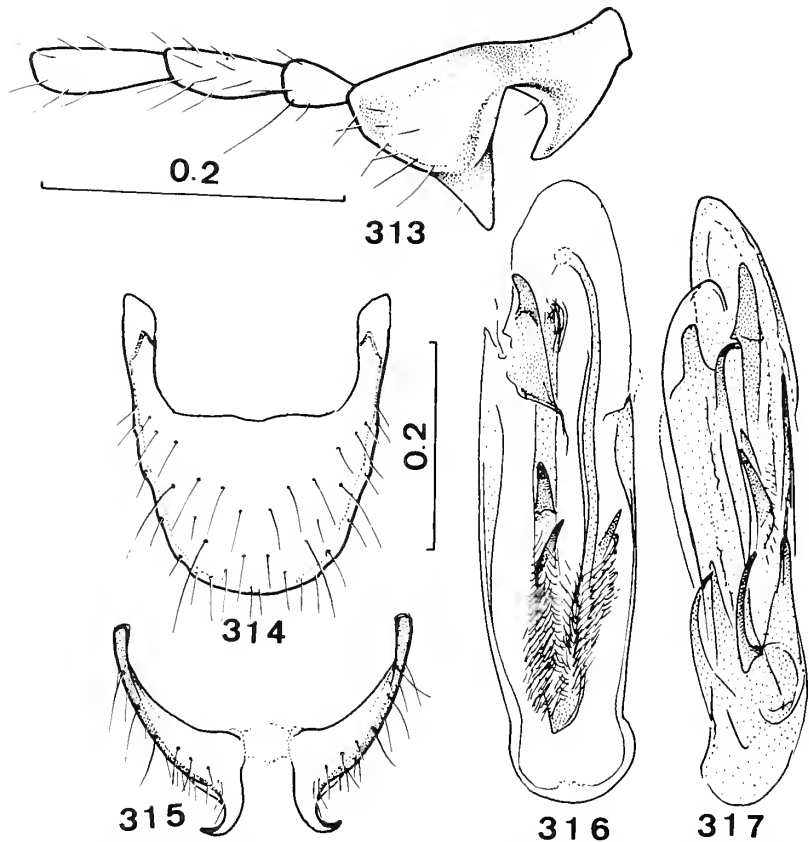


Abb. 313-317. *Sphinginopalpus* s.str. *bidens* Champion ♂: 313, Fühlerglieder 1-4; 314, Tergit 8; 315, Sternit 8; 316-317, Kopulationsapparat (316, dorsal; 317, Profil). Massstab von 314 auch für 315 und 313 auch für 316, 317.

51. *Sphinginopalpus* s. str. *dwesaensis* sp. nov.

MÄNNCHEN (Abb. 318-324).

Länge 2,5 mm.

Kopf inklusive der Wangen schwarz, von der Mitte der Augen nach vorne gelb, oder die gelbe Farbe liegt zwischen den Fühlerwurzeln nach vorne und neben jedem Auge befindet sich ein kleiner, verschwommener, gelber Flecken; Maxillarpalpen braun bis schwärzlich; Fühler schwarz, Glieder 1 bis 5 oder 6 gelb, 1 mehr oder weniger breit schwarz auf der Oberseite; Halsschild schwarz, der ganze abgeflachte Teil ist gelbbraun; Schildchen und Flügeldecken schwarz; letztere mit einem weisslichen Seitenflecken, der wenig nach vorne, jedoch lang und schmal nach hinten verlängert ist; Hinterbeine schwarz, Hinterschienen an der Basis kurz aufgeheilt, Hintertarsen gelb, 4 Vorderschenkel schwärzlich, oder mehr oder weniger aufgeheilt, 4 Vordertibien und 4 Vordertarsen gelb.

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

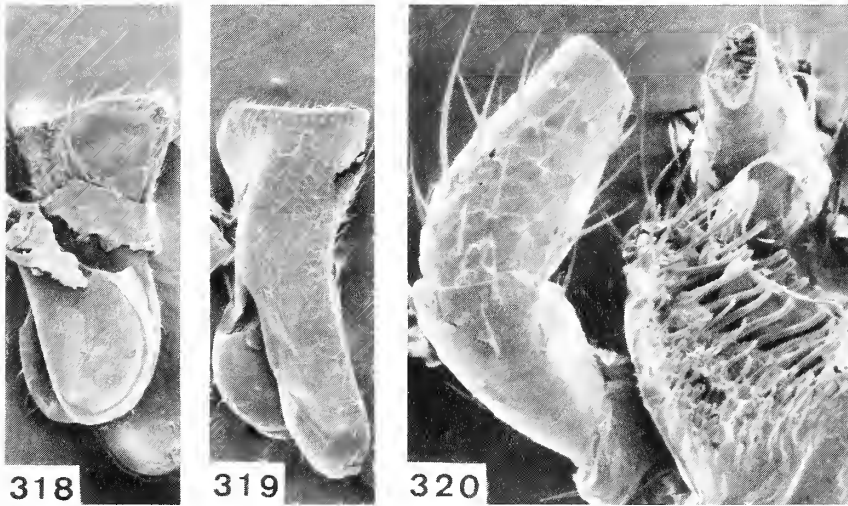


Abb. 318-320. *Sphinginopalpus* s. str. *dwesaensis* sp. nov. ♂: 318-319, Maxillarpalpen (x130) (318, von oben; 319, von unten); 320, Labialpalpen und Maxille (x550).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 318-319, Labialpalpen und Maxille Abb. 320. Fühler (Abb. 321) um 1/5 kürzer als die Flügeldecken, Glieder 3 bis 10 fast parallel, 3 nur wenig länger als 4. Halsschild länger als breit (17,5x15), sonst wie bei *capensis*, jedoch Oberfläche glatt, nur die abgeflachte Basis chagriniert. Flügeldecken langoval, wie bei *capensis*, etwas stärker punktiert; falsche Epipleuren ca. 80% der Länge einnehmend, nicht krenuliert. Tergit 8 Abb. 322. Sternit 8 Abb. 323.

Kopulationsapparat Abb. 324 dorsal.

Holotypus und 2 Paratypen (TMP): Transkei: Dwesa Forest, coast, grassnetting, dusk, 32°17'S, 28°50'E, 26.ii.1985, E-Y:2168, S. Endrödy-Younga. Transvaal: Irene, iii.1990, van Viegen, 1 Paratypus (NHMB); Rivonia, 23.-27.x.1968, M. I. Russell, 2 Paratypen (BM), 1 Paratypus (NHMB).

Diese neue Art ist neben *nigriceps* Wittmer zu stellen, von der sie sich hauptsächlich durch den verschiedenen Bau der Terminalia und des Kopulationsapparates unterscheidet.

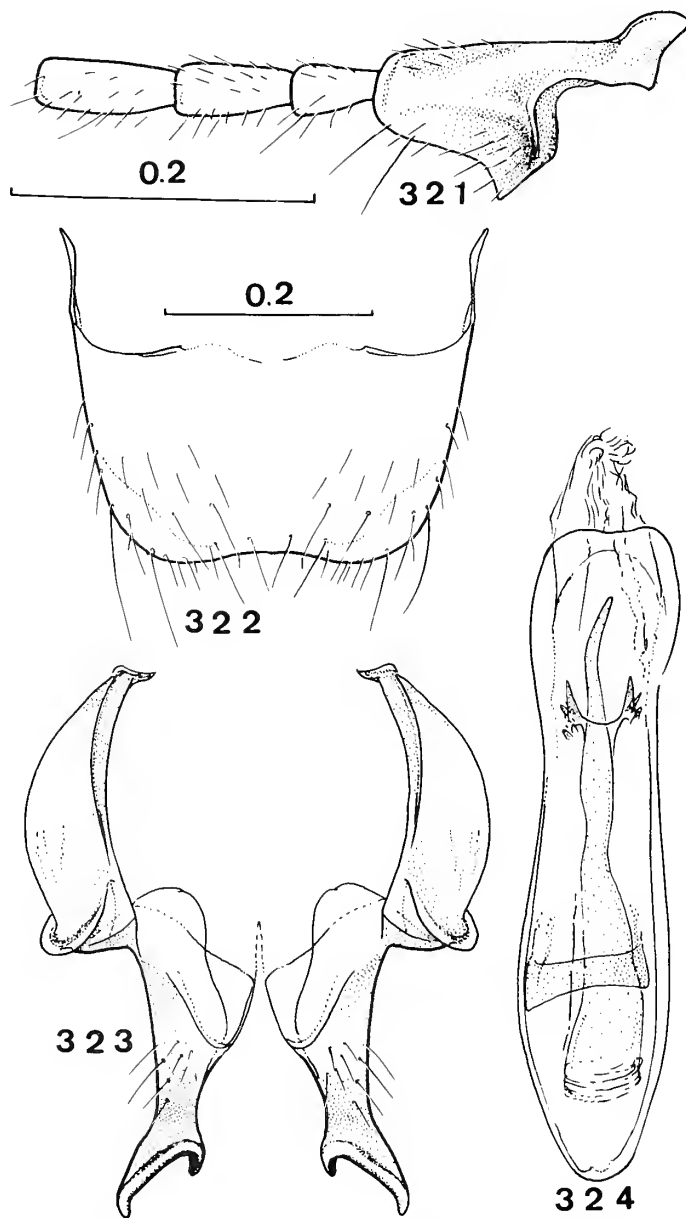


Abb. 321-324. *Sphinginopalpus* s. str. *dwesaensis* sp. nov. ♂: 321, Fühlerglieder 1-4; 322, Tergit 8; 323, Stermit 8; 324, Kopulationsapparat (dorsal). Massstab von 321 auch für 323, 324.

52. *Sphinginopalpus* s. str. *nigriceps* sp. nov.

MÄNNCHEN (Abb. 325-330).

Länge 2,3-2,5 mm.

Kopf schwarz; Maxillarpalpen schwarz, oder teilweise leicht aufgehellt; Fühler schwärzlich,



Abb. 325-326. *Sphinginopalpus* s. str. *nigriceps* sp. nov. ♂: 325-326, Maxillarpalpen (x200) (325, von oben, 326, von unten).

Glieder 1 bis 5 oder 6 gelb, 1 und 2 auf der Oberseite basal oder ganz dunkel; Halsschild schwarz; Flügeldecken mit einem weissen, dreieckigen Flecken jederseits, die Naht nicht erreichend, an den Seiten beidseitig verlängert; Hinterbeine schwarz bis dunkelbraun, 4 Vordersehenkel mehr oder weniger angedunkelt, 4 Vorderbeine oft ganz gelb, alle Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 325-326. Fühler (Abb. 327) um ca. 1/5 kürzer als die Flügeldecken, Glied 3 nur ganz wenig länger als 4, 2

bis 10 zur Spitze sehr wenig verbreitert. Halsschild länger als breit (19x15), sonst mit *capensis* übereinstimmend, jedoch aufgewölbter Teil glatt, abgeflachter chagriniert. Flügeldecken wie bei *capensis*, jedoch falsche Epipleuren ca. 60% der Länge der Decken einnehmend, kaum merklich krenuliert, nur wenige lange, helle, aufstehende Haare vorhanden. Tergit 8 Abb. 328. Sternit 8 Abb. 329.

Kopulationsapparat Abb. 330 dorsal.

Holotypus (TMP), 1 Paratypus (NHMB): South Africa: Transvaal: Nelshoogte, Knuckles grassveld, grassnetting, 25°47'S, 30°49'E, 24.x.1986, 4.xii.1986, E-Y:2312, 2350, S. Endrödy-Younga; Gods Window, grassnetting, 24°35'S, 30°51'E, 12.xi.1980, E-Y:1734, S. Endrödy-Younga, 1 Paratypus (TMP), 1 Paratypus (NHMB); Uitsoek, high altitude grassveld, grassnetting, 25°15'S, 30°34'E, 1500 m, 12.xii.1986, 6.ii.1987, E-Y:2381, 2426, S. Endrödy-Younga, 1 Paratypus (TMP), 1 Paratypus (NHMB).

Eine der wenigen Arten bei denen auch die ♀ einen einfarbig schwarzen Kopf besitzen. Das Fühlerglied 1 erinnert an *nelshoogtensis* Wittmer, neben den diese neue Art zu stellen ist.

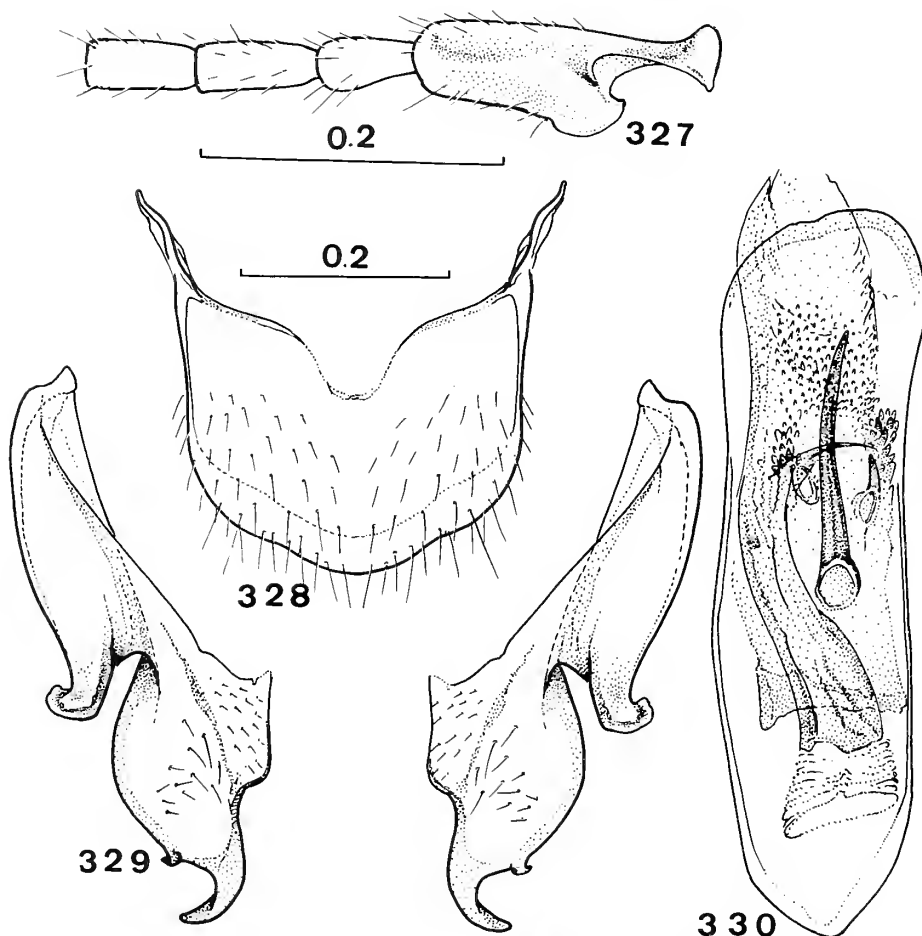


Abb. 327-330. *Sphinginopalpus* s. str. *nigriceps* sp. nov. ♂: 327, Fühlerglieder 1-4; 328, Tergit 8; 329, Sternit 8; 330, Kopulationsapparat (dorsal). Massstab von 327 auch für 329, 330.

53. *Sphinginopalpus* s. str. *uitsoekensis* sp. nov.

MÄNNCHEN (Abb. 331-336).

Länge 2,5 mm.

Kopf schwarz; Maxillarpalpen vorwiegend schwarz, teils etwas aufgehellte; Fühler gelb, Oberseite der Glieder 1 und 2 und 7 bis 11 schwarz; Halsschild schwarz, abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz; letztere mit einem weisslichen, leicht längsdreieckigen, seitlichen Flecken, dessen Spitze gegen die Naht gerichtet ist, ohne sie zu erreichen, er ist nach hinten etwas mehr als nach vorne verlängert, Totallänge wenig mehr als die Hälfte der Decken; Schenkel schwarz, die 4 vorderen gegen die Knie ein wenig aufgehellte, Hinterschienen schwarz, die mittleren auf der

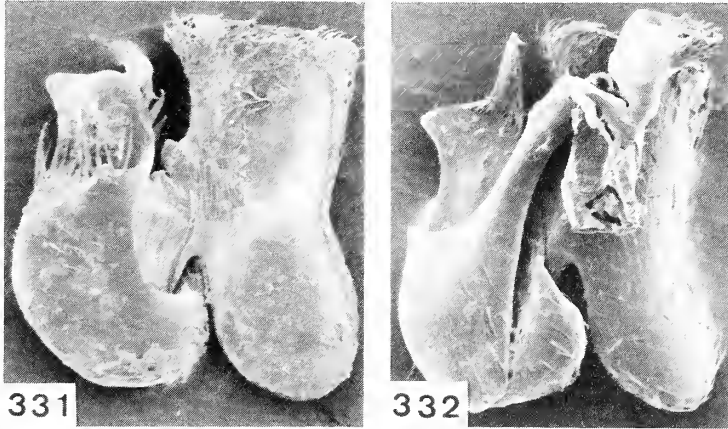


Abb. 331-332. *Sphinginopalpus* s. str. *uitsoekensis* sp. nov. ♂: 331-332, Maxillarpalpen (x170).

unteren Hälfte, die vorderen fast ganz hell, Tarsen gelb, nur die hinteren leicht angedunkelt.

Kopf mit den Augen nur wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 331-332. Fühler (Abb. 333) um ca. 1/4 kürzer als die Flügeldecken, Glieder 3 und 4 gleich lang. Halsschild länger als breit (17x15), sonst wie bei *elongatidens*, aufgewölbter Teil glatt, abgeflachter sehr schwach chagriniert. Flügeldecken langoval, falsche Epipleuren ca. 60% der Länge einnehmend, nicht krenuliert; Punktreihen von unterschiedlicher Regelmässigkeit, Punkte auf den letzten 1/3 fast verschwindend. Tergit 8 Abb. 334. Sternit 8 Abb. 335.

Kopulationsapparat Abb. 336 dorsal.

WEIBCHEN.

Wie das ♂ gefärbt, bei einem Exemplar sind die letzten Fühlerglieder aufgehell und die dunkle Färbung auf 1 und 2 fehlt.

Holotypus ♂ und 2 Paratypen ♀ (TMP), 1 Paratypus ♀ (NHMB): South Africa, E Transvaal: Uitsoek Forest Station, 1100 m, grassnetting, 25°18'S, 30°55'E, 13.xii.1986, E-Y:2384, S. Endrödy-Younga.

Neben *nigriceps* Wittmer zu stellen, mit dem diese neue Art nahe verwandt ist, beide haben einen schwarzen Kopf und ein ähnlich gebautes Fühlerglied 1, jedoch sehr verschiedene Terminalia.

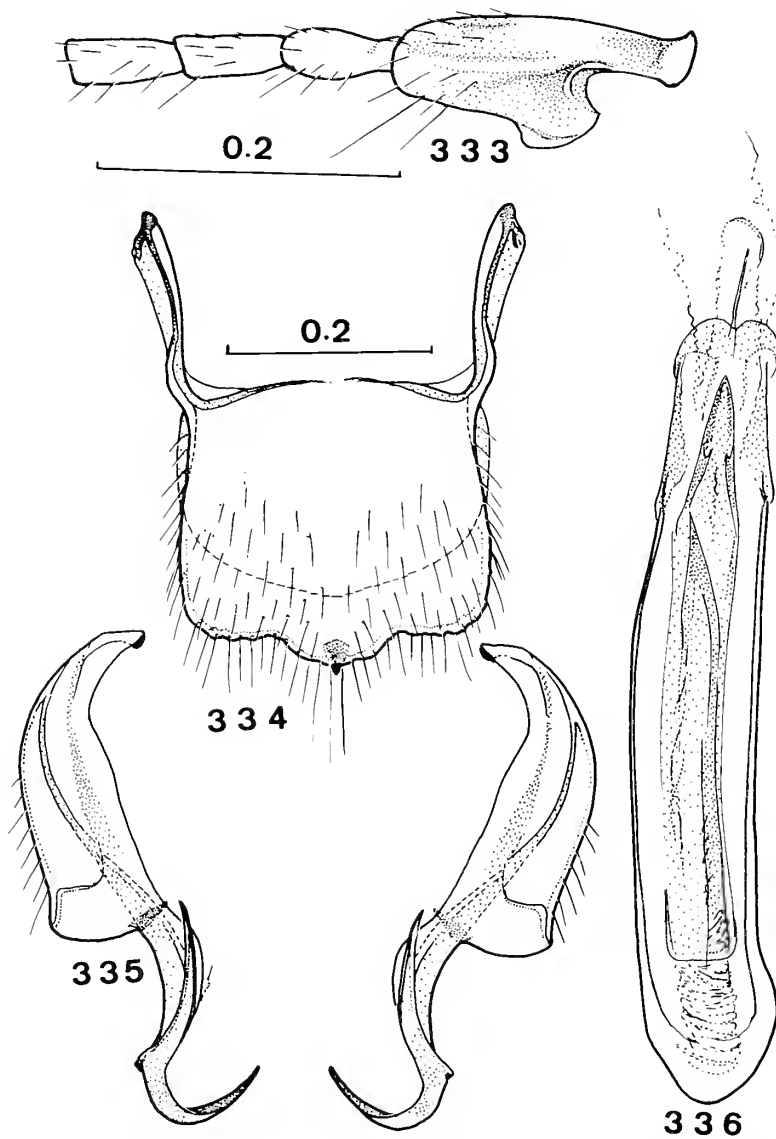


Abb. 333-336. *Sphinginopalpus* s. str. *uitsoekensis* sp. nov. ♂: 333, Fühlerglieder 1-4; 334, Tergit 8; 335, Sternit 8; 336, Kopulationsapparat (dorsal). Massstab von 333 auch für 335, 336.

54. *Sphinginopalpus* s. str. *curvispinus* sp. nov.

MÄNNCHEN (Abb. 337-341).

Länge knapp 3 mm.



Abb. 337. *Sphinginopalpus* s. str. *curvispinus* sp. nov. ♂: 337, Maxillarpalpus (x170) (von unten).

Kopf inklusive der Wangen schwarz, von der Mitte der Augen nach vorne gelb; Maxillarpalpen schwarz; Fühler schwarz, Glieder 1 bis 4 gelb, 1 und 2 auf der Oberseite teils ganz schwach angedunkelt; Halsschild schwarz, Basis schmal aufgeheilt; Schildchen und Flügeldecken schwarz, letztere jederseits mit einem dreieckigen, antimedialen, weissen Flecken, der sich gegen die Naht ausdehnt, ohne sie zu erreichen; Beine schwarz.

Kopf mit den Augen breiter als der Halsschild, Stirne ziemlich flach; Vorderstirne leicht gewölbt und erhöht, gegen die Stirne durch einen leicht gebogenen Wall von der Mitte der Augen an abgegrenzt, der die Grenze bildet zwischen der schwarzen und der gelben Färbung. Maxillarpalpen Abb. 337. Fühler (Abb. 338) um ca. 1/5 kürzer als die Flügeldecken, Zahn an Glied 1 sehr lang, Spitze leicht gebogen, 3 kaum merklich länger als 4. Halsschild länger als breit (21x17), sonst wie bei *tridensminus*, nur dass der abgeflachte Teil chagrinierter ist. Flügeldecken langoval; falsche Epipleuren ca. 55% der Länge einnehmend, Krenulierung kaum wahrnehmbar; Punktierung ähnlich wie *elongatidens*. Tergit 8 Abb. 339. Sternit 8 Abb. 340.

Kopulationsapparat Abb. 341 dorsal.

Holotypus (NHMB): South Africa, Natal: Elandskop, ca. 40 km W Pietermaritzburg, 2930 CA, 10.ix.1979, rocky ridge, grassland and proteas, J. Londt.

Diese neue Art zeichnet sich durch den besonderen Bau des Kopfes und den langen, leicht gebogenen Zahn an Fühlerglied 1 aus. Sie ist neben *longidens* Wittmer zu stellen.

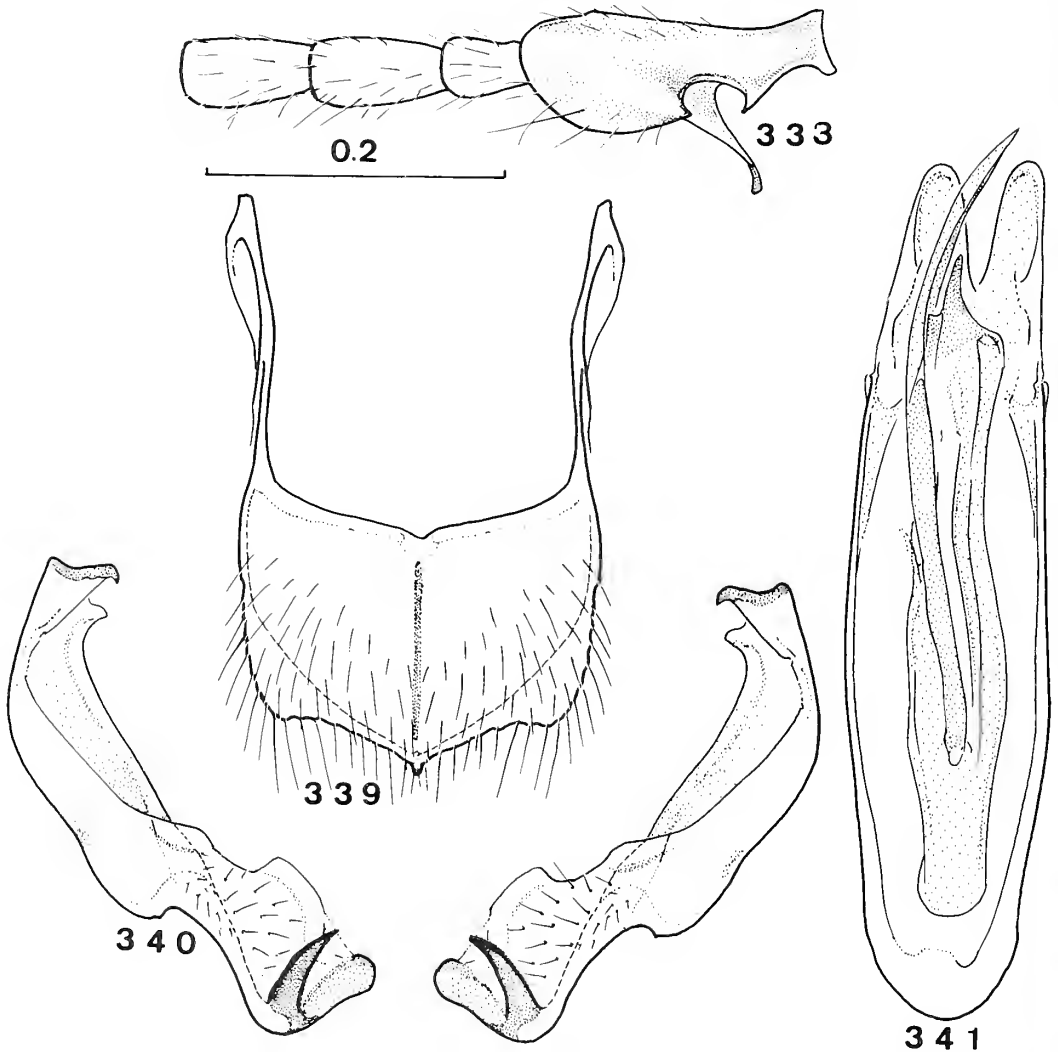


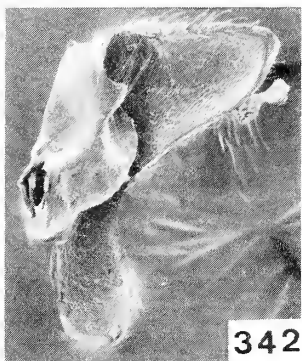
Abb. 338-341. *Sphinginopalpus* s. str. *curvispinus* sp. nov. ♂: 338, Fühlerglieder 1-4; 339, Tergit 8; 340, Sternit 8; 341, Kopulationsapparat (dorsal). Massstab von 338 auch für 339-341.

55. *Sphinginopalpus* s. str. *acutispinus* sp. nov.

MÄNNCHEN (Abb. 342-347).

Länge 2 mm.

Kopf inklusive der Wangen schwarz, von der Mitte der Augen nach vorne gelb; Maxillarpalpen gelbbraun, gegen die Spitzen der Glieder 1 und 2 aufgedunkelt; Fühler dunkel, basale 5 Glieder gelb;



342



343

Abb. 342-343. *Sphinginopalpus* s. str. *acutispinus* sp. nov. ♂: 342-343, Maxillarpalpen (x170) (342, von oben; 343, von unten).

Halsschild schwarz, ein Teil der abgesetzten Basis aufgeheilt; Schildchen und Flügeldecken schwarz, letztere jederseits mit einem antimedianen, dreieckigen, weisslichen Flecken; Hinterbeine schwarz mit leicht helleren Tarsen, 4 vordere Schenkel dunkel, gegen die Knie kurz aufgeheilt, vordere 4 Tibien und Tarsen hellbraun oder gelblich.

Kopf mit den Augen ein wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche

glatt, Chagrinierung kaum angedeutet. Maxillarpalpen Abb. 342-343. Fühler (Abb. 344) um ca. 1/5

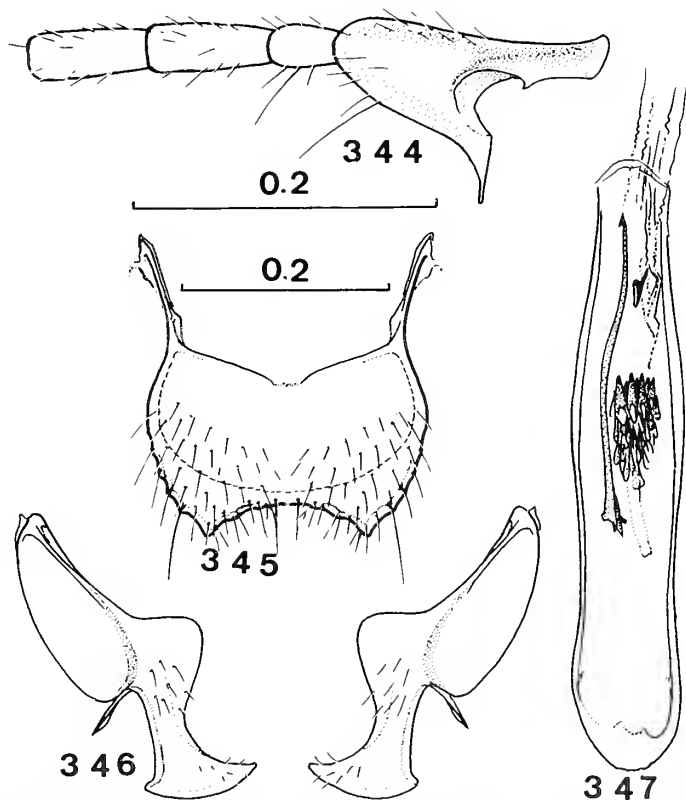


Abb. 344-347. *Sphinginopalpus* s. str. *acutispinus* sp. nov. ♂: 344, Fühlerglieder 1-4; 345, Tergit 8; 346, Sternit 8; 347, Kopulationsapparat (dorsal). Massstab von 344 auch für 346, 347.

kürzer als die Flügeldecken, Zahn auf Glied 1 besonders lang und schmal, 3 kaum merklich länger als 4. Halsschild langoval; falsche Epipleuren ca. 60% der Länge einnehmend, Krenulierung angedeutet; Punktierung ähnlich wie bei *oculimaculatus*. Tergit 8 Abb. 345, Sternit 8 Abb. 346.

Kopulationsapparat Abb. 347 dorsal.

Holotypus (TMP): South Africa, Cape Prov.: Amatole, Isidenge Forest Station, grass tussocks, 32°41'S, 27°15'E, 18.xi.1987, E-Y:2524, S. Endrödy-Younga.

Eine weitere neue Art mit langem Zahn auf Fühlerglied 1, die jedoch hinreichend durch die verschiedene Form des Zahnes, die Terminalia und den Kopulationsapparat von den anderen differenziert ist.

56. *Sphinginopalpus* s. str. *majeri* sp. nov.

MÄNNCHEN (Abb. 348-355).

Länge 2-2,2 mm.



Abb. 348-349. *Sphinginopalpus* s. str. *majeri* sp. nov. ♂: 348-349, Maxillarpalpen (x155) (348, von oben; 349, von unten).

Kopf schwarz mit einem fast viereckigen gelben Flecken auf dem Vorderkopf, der knapp die Mitte der Augen erreicht, ohne sie zu berühren; Maxillarpalpen braun; Fühler schwarz, Glied 1 auf der Unterseite und 2 bis 5 ganz gelb; Halsschild schwarz, ganzer abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz, letztere jederseits mit einem antimedialen, weisslichen Flecken, der die Naht nicht erreicht und an den Seiten etwas mehr nach hinten als

nach vorne verlängert ist. Hinterbeine schwarz, Hinterschienen gegen die Knie und Tarsen aufgeheilt; die 4 Vorderbeine gelb mit den Schenkeln zum grössten Teil schwarz.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 348-349. Fühler (Abb. 350) um ca. 1/5 kürzer als die Flügeldecken, Glied 1 nach dem Zahn nur wenig gegen die Spitze verjüngt, fast parallel, Zahn fast quadratisch, 3 nur wenig länger als 4. Halsschild länger als breit (18x15), Seiten auf dem vorderen Teil nur wenig nach vorne gerundet verengt; Oberfläche auf dem aufgewölbten Teil glatt, abgeflachte Basis fein chagrinirt. Flügeldecken langoval, falsche Epipleuren ca. 65% der Länge einnehmend, nicht krenuliert; Punktreihen bis zur Mitte ziemlich regelmässig, grobe Punkte ziemlich dicht, dann spärlicher, immer mehr erlöschend, Spitze glatt. Tergit 8 Abb. 352. Spiculum Abb. 353.

Kopulationsapparat Abb. 354 dorsal, Abb. 355 Profil.

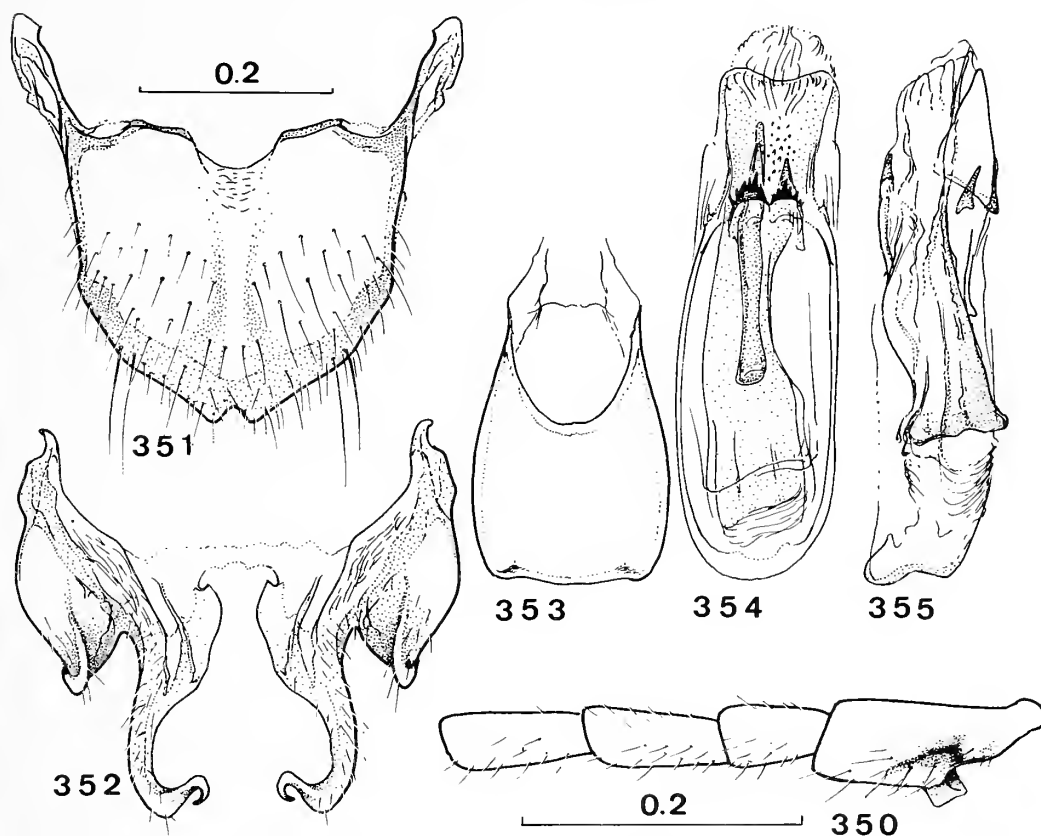


Abb. 350-355. *Sphinginopalpus* s. str. *majeri* sp. nov. ♂: 350, Fühlerglieder 1-4; 351, Tergit 8; 352, Sternit 8; 353, Spiculum; 354-355, Kopulationsapparat (354, dorsal; 355, Profil). Massstab von 351 auch für 352-355.

WEIBCHEN.

Kopf einfarbig schwarz; Fühlerglied 1 nur an der Basis kurz, leicht angedunkelt; Flügeldecken ohne Quermakel, Seitenbänder etwas verbreitert; Punktierung weniger stark.

Holotypus ♂ und 2 Paratypen (BM), 1 Paratypus ♀ (NHMB): Zimbabwe: Salisbury (jetzt Harare), Mashonaland, MCH. (March ?), G. A. K. Marshall.

Es freut mich, diese Art meinem lieben Kollegen, Karel Majer, Brno, widmen zu dürfen, dem ich die zahlreichen Abbildungen in dieser Publikation verdanke.

Diese Art wurde von Champion (1927) als *oneili* Pic bestimmt. Die Maxillarpalpen zeigen wenig Unterschiede zu *oneili*, unsomehr sind die Fühler, die Terminalia und der Kopulationsapparat verschieden.

57. *Sphinginopalpus s. str. expansus* sp. nov.

MÄNNCHEN (Abb. 356-357).

Länge 2,7 mm.

Eine äusserlich mit *oculimaculatus* Wittmer übereinstimmende Art, es erübrigt sich, sie noch einmal zu beschreiben. Auch die Terminalia stimmen weitgehend mit *oculimaculatus* überein. Grosse Unterschiede zeigen die Maxillarpalpen (Abb. 356-357), sodass *expansus* ohne Zweifel als eigene Art gelten kann.



Abb. 356-357. *Sphinginopalpus s. str. expansus* sp. nov. ♂: Maxillarpalpen (x170) (356, von oben; 357, von unten).

Holotypus ♂ (TMP): South Africa, E Transvaal: Nelshoogte Forest Station, S. Endrödy-Younga.

58. *Sphinginopalpus s. str. oculimaculatus* sp. nov.

MÄNNCHEN (Abb. 358-364).

Länge 2,7 mm.

Kopf schwarz mit einem kleinen gelblichen Flecken neben jedem Auge über der Fühlerwurzel; Maxillarpalpen schwarz; Fühler schwarz, die ersten 5 Glieder gelb, 1, manchmal auch 2 ganz wenig und 5 auf der Oberseite angedunkelt; Halsschild schwarz, Basis kurz gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einer antimedialen Quermakel, die an der Naht unterbrochen ist und sich an den Seiten wenig ausdehnt; Hinterschenkel schwarz, die 4 vorderen braun, an der Basis ein wenig dunkler, Hintertibien und Tarsen dunkel, die 4 vorderen mehr oder weniger aufgehellt.

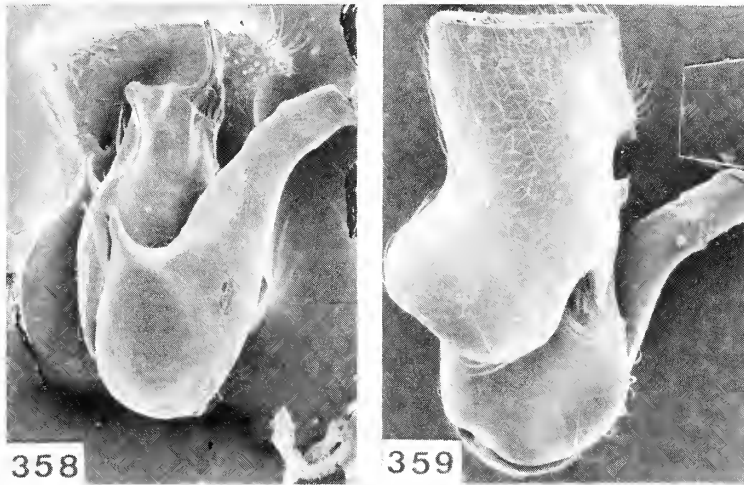


Abb. 358-359. *Sphinginopalpus* s. str. *oculimaculatus* sp. nov. ♂: Maxillarpalpen (x155)
(358, von oben; 359, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche auf der Stirne glatt, nach vorne schwach chagriniert. Maxillarpalpen Abb. 358-359. Fühler (Abb. 360) um ca. 1/10 kürzer als die Flügeldecken, Glied 3 deutlich länger als breit (21x17); Oberfläche glatt, abgeflachter Teil chagriniert, sonst wie *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, nicht krenuliert; Punktreihen nicht ganz regelmässig, Punkte nach hinten weniger tief und auf dem letzten 1/4 fast ganz erloschen. Tergit 8 Abb. 361. Sternite 7 und 8 Abb. 362 und 363.

Kopulationsapparat Abb. 364 dorsal.

WEIBCHEN.

In der grossen Serie von Nelshoogte befand sich kein ♀, wahrscheinlich weil bis auf 2 Exemplare alle am Auto abgelesen wurden, wo sie angefliegen kamen. Ein ♀ befand sich unter dem Material aus Berlin, das ich jedoch wegen der abweichenden hellen Färbung der Beine und auch wegen den etwas helleren Flügeldecken nur mit Vorbehalt zu dieser Art stelle.

Holotypus und 162 Paratypen (TMP), 31 Paratypen (NHMB), 6 Paratypen (AMG): South Africa, E Transvaal: Nelshoogte Forest Station, grassnetting, beating, but attracted to the car in big number, 25°47'S, 30°50'E, 1.xii.1986, E-Y:2336, 2337, 2339, S. Endrödy-Younga; Berlin Forest Station, 1500 m, grassnetting 25°32'S, 30°44'E, E-Y:2360, 7.xii.1986, S. Endrödy-Younga, 5 Paratypen (TMP), 2 Paratypen (NHMB).

Neben *acutispinus* Wittmer zu stellen, dessen Fühlerglied 1 sehr ähnlich gebaut ist, sonst aber durch die glatten, etwas weniger dicht punktierten Flügeldecken und die Terminalia sehr verschieden.

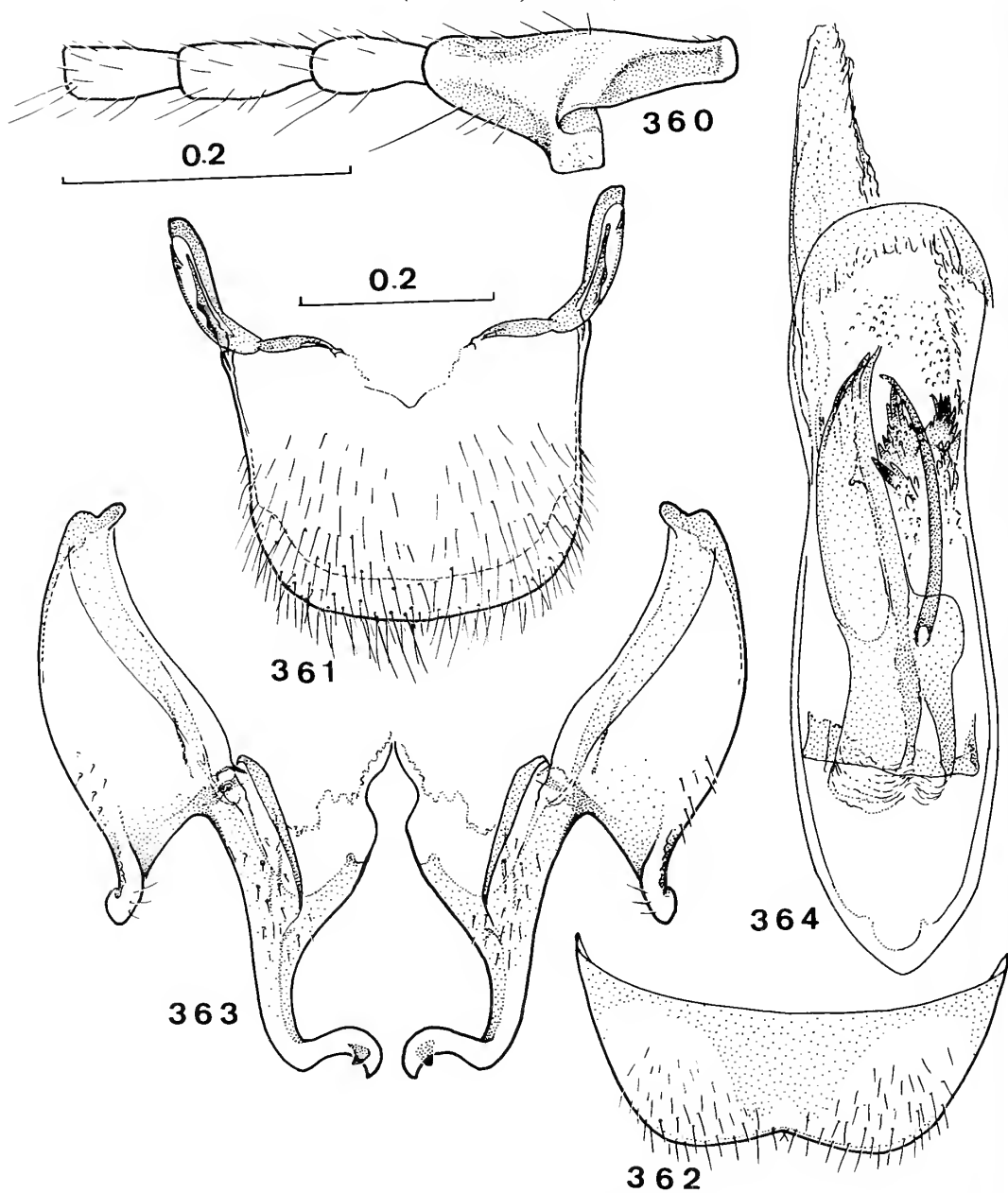


Abb. 360-364. *Sphinginopalpus* s. str. *oculimaculatus* sp. nov. ♂: 360, Fühlerglieder 1-4; 361, Tergit 8; 362, Sternit 7; 363, Sternit 8; 364, Kopulationsapparat (dorsal). Massstab von 360 auch für 363, 364 und 361 auch für 362.

59. *Sphinginopalpus* s. str. *zulu* sp. nov.

MÄNNCHEN (Abb. 365-370).

Länge 2,1 mm.

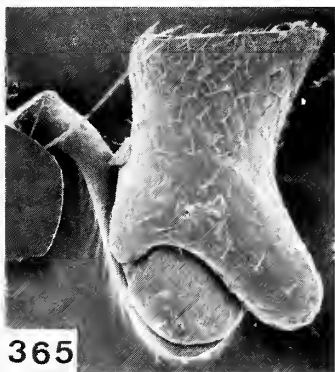


Abb. 365. *Sphinginopalpus* s. str. *zulu* sp. nov. ♂: 365, Maxillarpalpus (x170) (von unten).

Kopf schwarz, Vorderkopf um die Fühlerwurzeln und Wangen leicht aufgehell; Maxillarpalpen gelbbraun; Fühler gelb, die letzten 5 bis 6 Glieder, sowie die Oberseite von 1 verschwommen schwärzlich; Halsschild schwarz, ca. die Hälfte des abgeflachten Teils gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem ziemlich breiten, weisslichen, antimedialen Querband, das an der Naht unterbrochen und an den Seiten ein wenig verlängert ist; Hinterbeine schwarz, Tarsen ein wenig aufgehell, Schenkel und Schienen der 4 vorderen Beine dunkel, teils aufgehell, die 4 vorderen Tarsen gelb, letztes Glied leicht angedunkelt.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpus Abb. 365. Fühler (Abb. 366) um ca. 1/5 kürzer als die Flügeldecken, Glied 3 deutlich länger als 4, fast doppelt so lang wie 2. Halsschild länger als breit (18x15); Oberfläche glatt, abgeflachter Teil chagriniert, sonst wie *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 70%

der Länge einnehmend, ungefähr in der Mitte, kurz, ganz fein krenuliert; Punktierung in Punktreihen, die nicht ganz regelmässig sind, Punkte gegen die Spitze fast erlöschend. Tergit 8 Abb. 367. Sternite 7 und 8 Abb. 368 und 369.

Kopulationsapparat Abb. 370 dorsal.

Holotypus (TMP): South Africa, Zululand: Lake Bhangasi, grassnetting, 28°07'S, 32°31'E, 18.xii.1976, E-Y:982, S. Endrödy- Younga.

Diese neue Art ist mit *albilabris* (Boheman) und *variceps* Wittmer verwandt, Fühlerglied 1 ähnlich, Terminalia sehr verschieden, vergleiche Abbildungen.

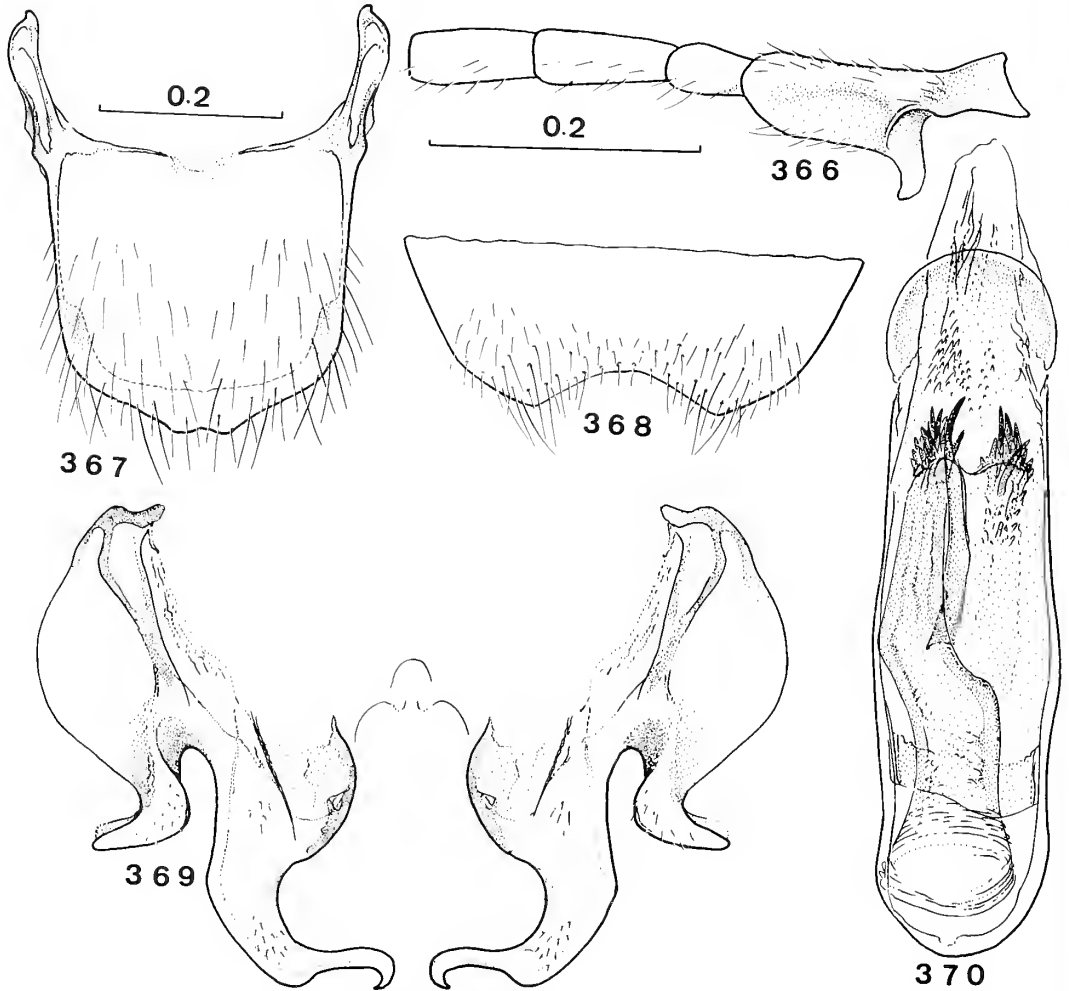


Abb. 366-370. *Sphinginopalpus* s. str. *zulu* sp. nov. ♂: 366, Fühlerglieder 1-4; 367, Tergit 8; 368, Sternit 7; 369, Sternit 8, 370, Kopulationsapparat (dorsal). Massstab von 366 auch für 369, 370 und 367 auch für 368.

60. *Sphinginopalpus* s. str. *politus* sp. nov.

MÄNNCHEN (Abb. 371-376).

Länge 2,2-2,3 mm.

Kopf schwarz, nur die Wangen schmal bis zu den Augen, seltener nur der Vorderkopf schmal gelb; Maxillarpalpen schwärzlich; Fühler schwarz, die ersten 5 Glieder gelb, mit der Basis von 1 schwarz, oft ist auch 6 an der Basis aufgehellte; Halsschild schwarz, Basis gelbbraun; Schildchen und

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

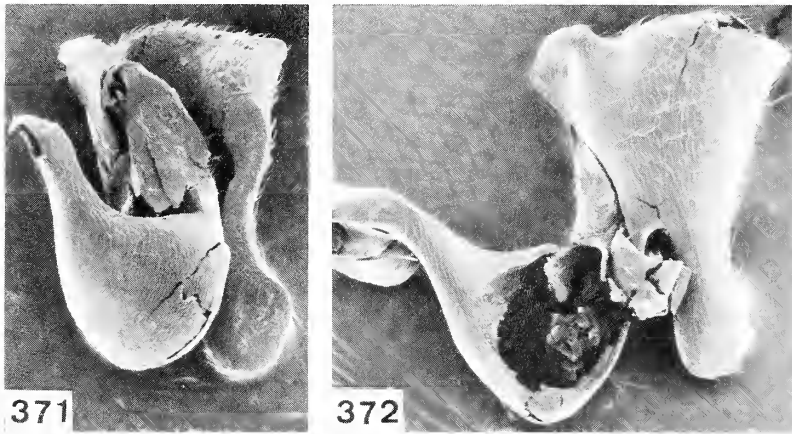


Abb. 371-372. *Sphinginopalpus* s. str. *politus* sp. nov. ♂: 371-372, Maxillarpalpen (x170) (371, von oben; 372, von unten, Glieder 1 und 2 zurückgelegt).

Flügeldecken schwarz, letztere mit einem durchgehenden, gelben Querband vor der Mitte, das sich an den Seiten verlängert; bei 1 Exemplar ist das Querband stark reduziert und an der Naht unterbrochen; 4 Hinterbeine schwarz, Spitzen der Mitteltibien mehr oder weniger aufgehellt, Tarsen meistens ganz aufgehellt, Vorderschenkel angedunkelt, Vordertibien fast ganz hell.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt, glänzend. Maxillarpalpen Abb. 371-372. Fühler (Abb. 373) um ca. 1/10 kürzer als die Flügeldecken, der kleine Zahn von Glied 1 nahe der Basis ist stark reduziert, vom grösseren Zahn ab ist das Glied fast parallel, 3 ein wenig länger als 4, 4 nach innen schwach gerundet erweitert. Halsschild länger als breit (17x13); Oberfläche glatt, glänzend, nur der abgeflachte Teil schwach chagriniert, sonst mit *capensis* übereinstimmend. Flügeldecken langoval, Krenulierung der falschen Epipleuren von variabler Stärke, manchmal so gering wie bei diesem; Punktierung wie bei diesem; Behaarung ebenso. Tergit 8 Abb. 374. Sternit 8 Abb. 375.

Kopulationsapparat Abb. 376 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz; Querband auf den Flügeldecken meistens an der Naht unterbrochen. Schulterbeulen nur wenig entwickelt; ungeflügelt.

Holotypus und 9 Paratypen (TMP), 4 Paratypen (NHMB): South Africa, SW Cape Prov.: Heuningnes River, 34°42'S, 20°02'E, 28.x.1983, E-Y:2028, 2029, S. Endrödy-Younga; Clanwilliam-Elandsbaai, 16.ix.1985, W. Wittmer, 1 Paratypus (NHMB); Verlorevlei farm, 32°19'S, 18°22'E, 28.viii.1981, E-Y:1857, S. Endrödy-Younga, 1 Paratypus (TMP), 1 Paratypus (NHMB).

Diese neue Art hat ein ähnlich paralleles Fühlerglied 1 mit kleinem Zahn wie *leucosideae* Wittmer, jedoch sehr verschieden gebaute Maxillarpalpen und Terminalia.

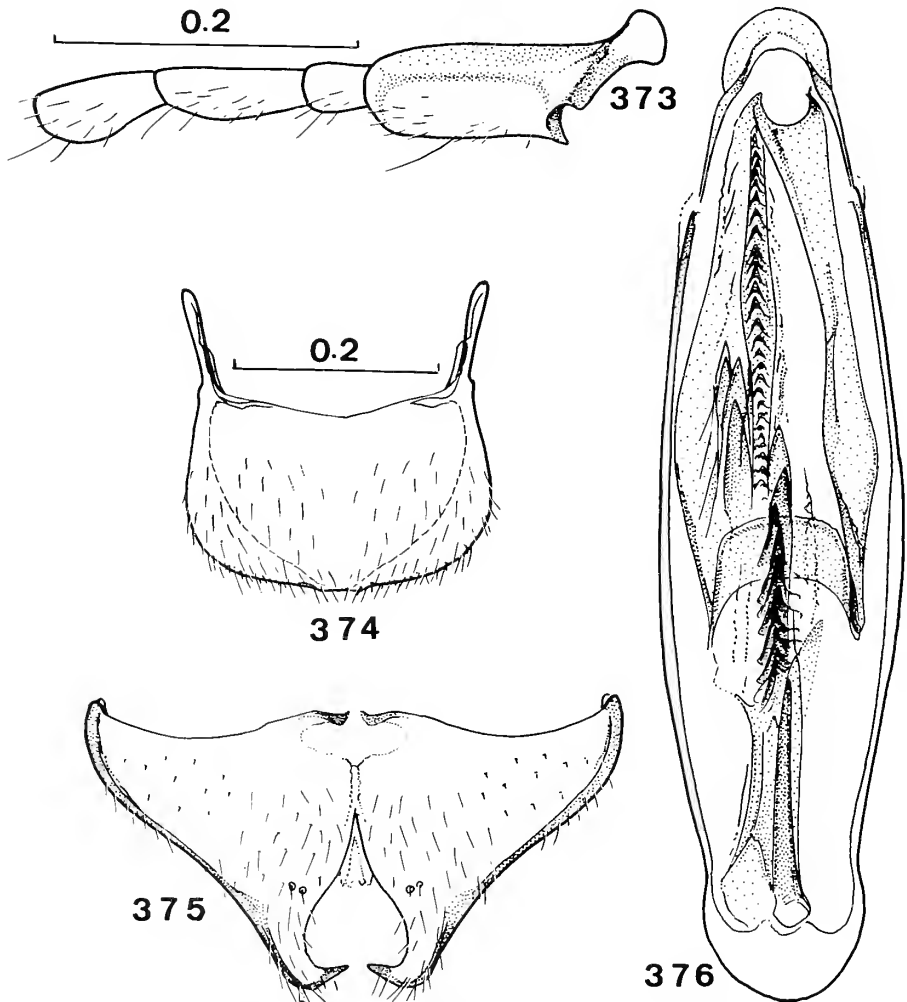


Abb. 373-376. *Sphinginalpalpus* s. str. *politus* sp. nov. ♂: 373, Fühlerglieder 1-4; 374, Tergit 8; 375, Sternit 8; 376, Kopulationsapparat (dorsal). Massstab von 373 auch für 375, 376.

61. *Sphinginalpalpus* s. str. *levemaculatus* sp. nov.

MÄNNCHEN (Abb. 377-383).

Länge 2,1 mm.

Kopf schwarz, über jeder Fühlerwurzel ein kleiner, verschwommener, heller Flecken; Maxillarpalpen schwarz; Fühler schwarz, die ersten 4 Glieder und die Basis von 5 gelb, 1 auf der Oberseite an der Basis angedunkelt; Halsschild schwarz, bei letzterem die Seiten, ungefähr in der

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

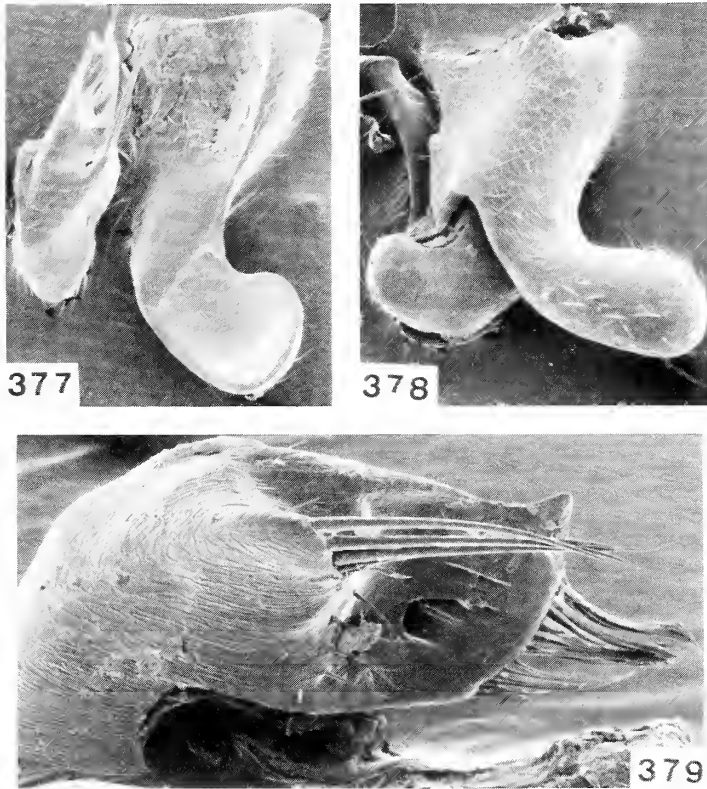


Abb. 377-379. *Sphinginopalpus* s. str. *levemaculatus* sp. nov. ♂: 377-379, Maxillarpalpen (377, von oben, x170; 378, von unten, x170; 379, Glied 2, x390).

Breite und Länge der falschen Epipleuren, weisslich; Hinterbeine schwarz, die 4 vorderen schwärzlich mit den Spitzen der Tibien und Tarsen angedunkelt.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 377-378. Fühler (Abb. 380) ca. um 1/5 kürzer als die Flügeldecken, Glieder 3 bis 10 fast parallel, 3 deutlich länger als 4. Halsschild länger als breit (17x13,5), sonst wie *capensis*, nur dass der aufgewölbte Teil glatt und der abgeflachte chagriniert ist. Flügeldecken langoval, ungefähr in der Mitte am breitesten; Schulterbeulen normal; falsche Epipleuren ungefähr 50% der Länge einnehmend, Krenulierung fehlt; Punkte wenig dicht und wenig tief, in Punktreihen; einzelne lange, aufrechtstehende Haare vorhanden. Tergit 8 Abb. 381. Sternit 8 Abb. 382.

Kopulationsapparat Abb. 383 Profil.

Holotypus (NHMB): South Africa, Cape Prov.: 5 km E Humansdorp, 7.xi.1988, W. Wittmer, M. J. D. Brendell.

Eine weitere Art mit langem Zahn auf Fühlerglied 1, sie kann neben *acutispinus* Wittmer and *longispinus* Wittmer gestellt werden, mit verschiedenen gebauten Terminalia und Kopulationsapparat.

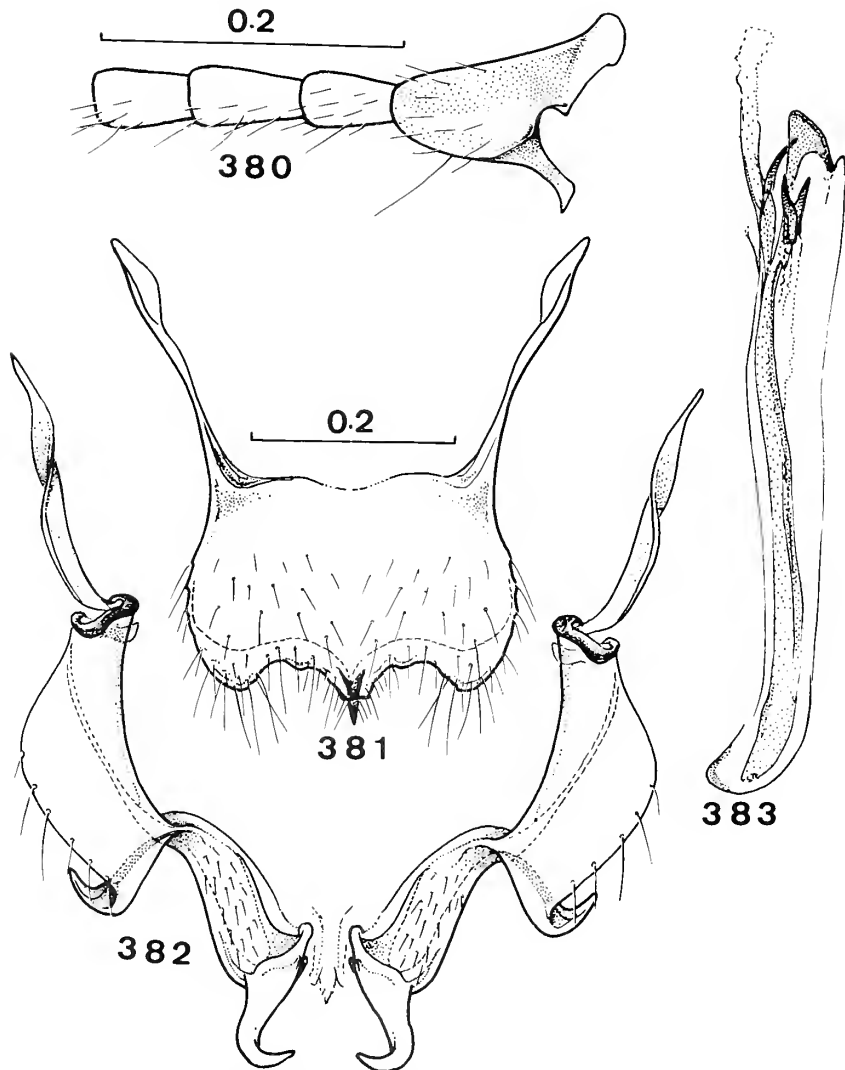


Abb. 380-383. *Sphinginopalpus* s. str. *levemaculatus* sp. nov. ♂: 380, Fühlerglieder 1-4; 381, Tergit 8; 382, Sternit 8; 383, Kopulationsapparat (Profil). Massstab von 380 auch für 382-383.

62. *Sphinginopalpus* s. str. *trispinus* sp. nov.

MÄNNCHEN (Abb. 384-389).

Länge 2,2 mm.

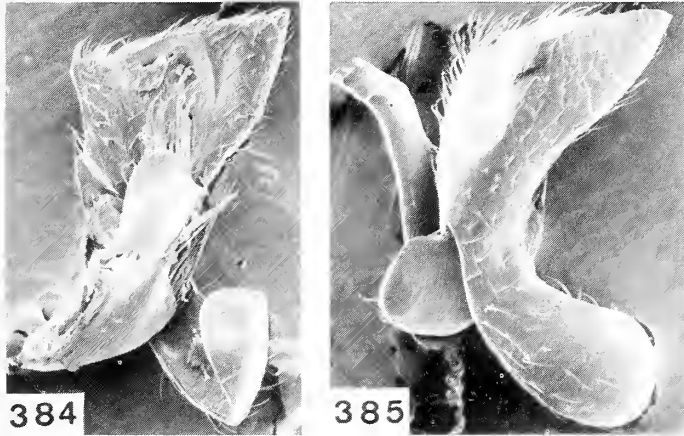


Abb. 384-385. *Sphinginopalpus* s. str. *trispinus* sp. nov. ♂: 384-385, Maxillarpalpen (x170) (384, von oben; 385, von unten).

Tarsen schwach heller, 4 Vorderschenkel schwarz, 4 Vorderschienen dunkel, an den Spitzen heller, 4 Vordertarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche fein chagriniert. Maxillarpalpen Abb. 384-385. Fühler (Abb. 386) um ca. 1/5 kürzer als die Flügeldecken, Glied 3 länger als 4, der dritte Zahn auf 1 ist nicht immer deutlich sichtbar (je nach Stellung). Halsschild länger als breit (21x15), Seiten nach vorne kaum merklich verengt; Oberfläche des aufgewölbten Teiles fast glatt, oder fein chagriniert, abgeflachter Teil chagriniert, sonst wie *elongatidens*. Flügeldecken langoval, falsche Epipleuren ca. 65% der Länge einnehmend, Krenulierung sehr fein; sonst wie *elongatidens*. Tergit 8 Abb. 387. Sternit 8 Abb. 388.

Kopulationsapparat Abb. 389 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz; Fühler ohne schwarzen Flecken auf Glied 3, sonst wie das ♂ gefärbt. Flügeldecken mit stärker gerundeten Seiten, Schulterbeulen nur angedeutet; ungeflügelt.

Holotypus und 5 Paratypen (TMP), 3 Paratypen (NHMB): South Africa, Natal Middld.: Karkloof grassveld with river, 29°19'S, 30°15'E, 7.xii.1989, E-Y:2747, 2758, S. Endrödy-Younga, l. Klimaszewski. Cape Prov.: Amatole, Isidenge Forest Station, grassnetting, indigenous forest and ground traps 25 days with faeces bait, 32°41'S, 27°14'-16'E, E-Y:2510, 2511, 2514, 2524, S. Endrödy-Younga, 3 Paratypen (TMP), 2 Paratypen (NHMB); idem, 8.xii.1987, E-Y:2559, S. Endrödy-Younga, netted and Arum flowers, 1 Paratypus (TMP).

Kopf schwarz, Wangen teilweise gelb, ein kleiner Flecken am Vorderkopf und je ein kleiner Flecken neben den Augen, gelb; Maxillarpalpen schwarz; Fühler schwärzlich, Glieder 1 bis 5 gelb, 1 an der Basis und 3 mit einem mehr oder weniger grossen Flecken oben; Halsschild schwarz, Basis fast bis zu 1/3 des abgeflachten Teiles gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem seitlichen, antimedialen, weisslichen Flecken, der die Naht nicht erreicht, am Seitenrand am breitesten; Hinterbeine schwarz,

Eine der wenigen Arten mit verbreitertem Fühlerglied 3 und sehr breitem 1, das Tergit 8 läuft in 3 Spitzen aus. Die neue Art is neben *productus* Wittmer zu stellen, Fühler und Sternit 8 sehr verschieden gebaut.

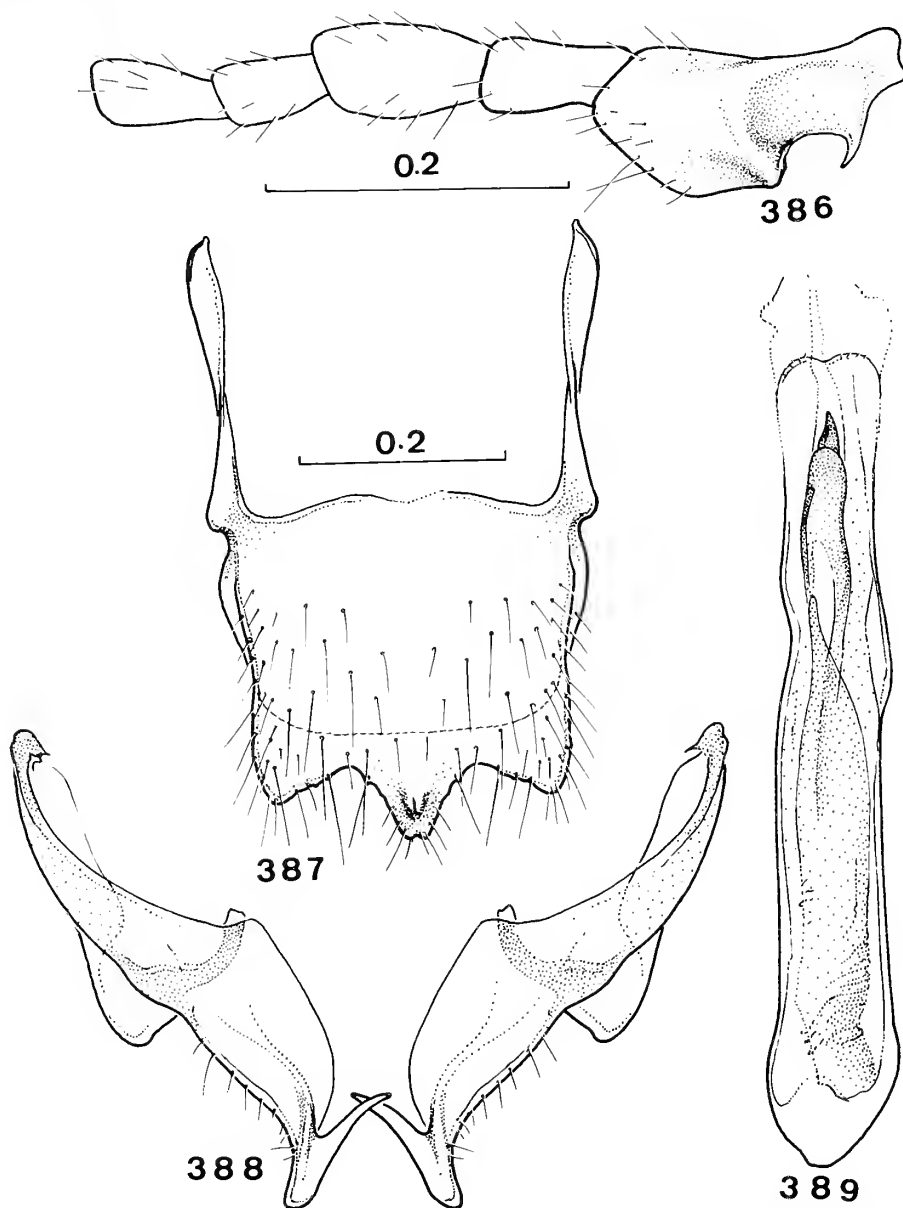


Abb. 386-389. *Sphinginopalpus* s. str. *trispinus* sp. nov. ♂: 386, Fühlerglieder 1-5; 387, Tergit 8; 388, Sternit 8; 389, Kopulationsapparat (dorsal). Massstab von 386 auch für 388, 389.

63. *Sphinginopalpus* s. str. *productus* sp. nov.

MÄNNCHEN (Abb. 390-395).

Länge knapp 2 mm.

Kopf schwarz, von der Mitte der Augen nach vorne mit den Wangen gelb; Maxillarpalpen vorwiegend gelb; Fühler gelb, letzte 4 bis 5 Glieder schwarz; Halsschild schwarz, abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz, letztere an den Seiten mit einem weisslichen, länglichen Flecken, der ungefähr die Hälfte der Länge einnimmt; Schenkel schwarz, die 4 vorderen gegen die Knie kurz gelb, Schienen gelb, die hinteren angedunkelt, Tarsen gelb, die hinteren etwas angedunkelt.

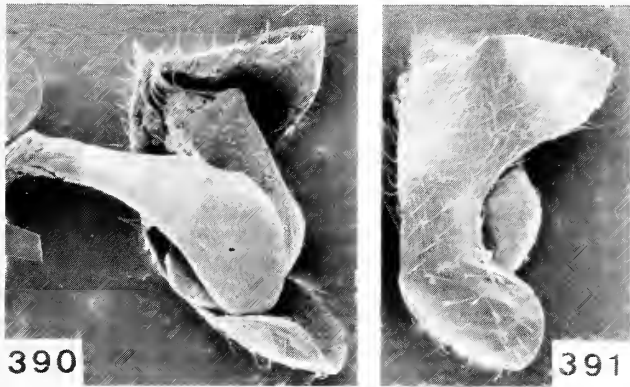


Abb. 390-391. *Sphinginopalpus* s. str. *productus* sp. nov. ♂: 390-391, Maxillarpalpen (x170) (390, von oben; 391, von unten).

Kopf mit den Augen etwas breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche an der Basis fein punktiert, dazwischen chagriniert. Maxillarpalpen Abb. 390-391. Fühler (Abb. 392) ca. 1/5 kürzer als die Flügeldecken, Glied 3 ein wenig länger als 4 (länger als auf der Abbildung gezeichnet). Halsschild wenig länger als breit (15x13,5), sonst wie bei *elongatidens*, aufgewölbter Teil glatt, abgeflachter chagriniert. Flügeldecken langoval, wie *elongatidens*, jedoch falsche Epipleuren kürzer, nur ca. 60% der Länge einnehmend, nicht krenuliert

und Punkte auf dem letzten Drittel fast ganz erloschen. Tergit 8 Abb. 393. Sternit 8 Abb. 394.

Kopulationsapparat Abb. 395 dorsal.

Holotypus und 1 Paratypus (TMP), 2 Paratypen (NHMB): South Africa, Natal: Weza, Impetyene grassland, grass tussocks, 30°37'S, 29°42'E, 25.xi.1989, E-Y:2718, S. Endrödy-Younga.

Diese neue Art ist neben *trispinus* Wittmer zu stellen, sie hat ein ähnlich gebautes Tergit 8, der Kopulationsapparat ist von einer einfacheren Bauart, die übrigen Merkmale wie Fühlerglied 1, Maxillarpalpen, Sternit 8 und der Kopulationsapparat sind sehr verschieden.

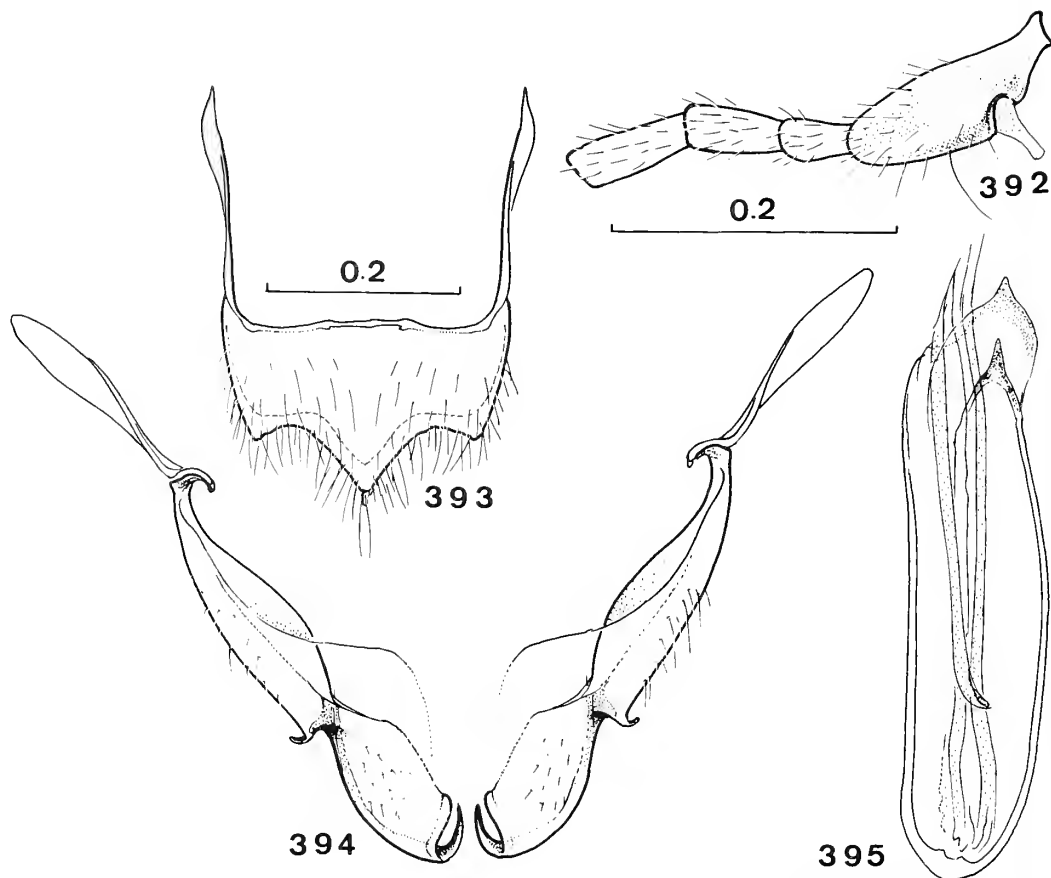


Abb. 392-395. *Sphinginopalpus* s. str. *productus* sp. nov. ♂: 392, Fühlerglieder 1-4; 393, Tergit 8; 394, Sternit 8; 395, Kopulationsapparat (dorsal). Massstab von 392 auch für 394, 395.

64. *Sphinginopalpus* s. str. *rudebecki* Wittmer

Sphinginopalpus rudebecki Wittmer, 1960: 117, figs 4-5.

MÄNNCHEN (Abb. 396-401).

Die Art ist seit ihrer Entdeckung nicht wieder gefunden worden. Um eine sichere Bestimmung zu ermöglichen, wurden noch folgende Aufnahmen und Zeichnungen angefertigt: Maxillarpalpen Abb. 396-397. Fühlerglieder 1 bis 4 Abb. 398. Tergit 8 Abb. 399. Sternit 8 Abb. 400. Kopulationsapparat Abb. 401 dorsal.

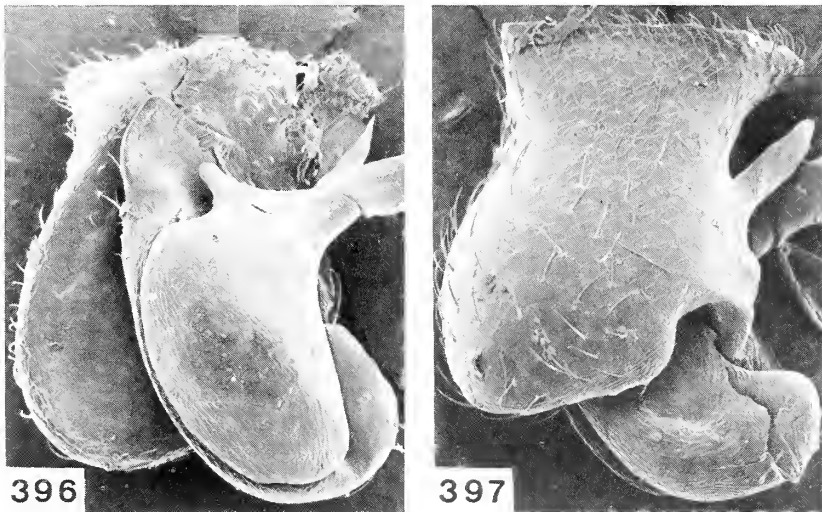


Abb. 396-397. *Sphinginopalpus* s. str. *rudebecki* Wittmer ♂: 396-397, Maxillarpalpen (x200) (396, von oben; 397, von unten).

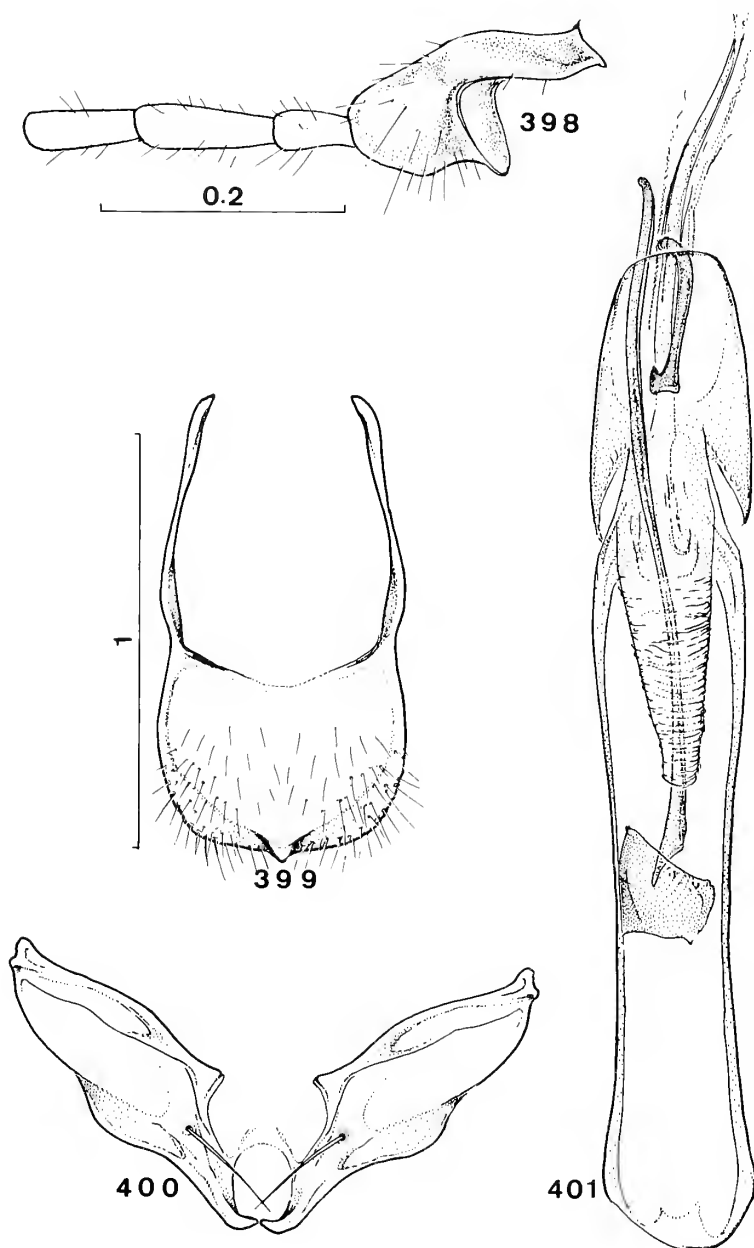


Abb. 398-401. *Sphinginopalpus* s. str. *rudebecki* Wittmer ♂: 398, Fühlerglieder 1-4; 399, Tergit 8; 400, Sternit 8; 401, Kopulationsapparat (dorsal). Massstab von 398 auch für 400, 401.

65. *Sphinginopalpus* s. str. *wezaensis* sp. nov.

MÄNNCHEN (Abb. 402-408).

Länge 3 mm.

Kopf schwarz, von der Mitte nach vorne mit den Wangen gelb; Glied 3 der Maxillarpalpen schwarz, 2 schwärzlich; Fühler gelb; Halsschild schwarz, Basis schmal gelbbraun; Schildchen



402



403



404

Abb. 402-404. *Sphinginopalpus* s. str. *wezaensis* sp. nov. ♂: 402-403, Maxillarpalpen (x130) (402, von oben; 403, von unten); 404, Maxille (x 525).

schwärzlich; Flügeldecken schwarz, Basis vor den Schultern kurz bräunlich, vor der Mitte ein gelbbraunes, schmales, leicht unduliertes, durchgehendes Querband, das an der Naht bis zum Schildchen verlängert ist; Schenkel schwarz, die vorderen an der Basis stärker als die hinteren aufgefellt, Vordertibien am wenigsten angedunkelt, die mittleren stärker, die hinteren ganz schwarz, alle Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche chagriniert. Maxillarpalpen Abb. 402-403. Maxille Abb. 404. Fühler (Abb. 405) ungefähr so lang wie die Flügeldecken, Zahn an der Basis von Glied 1 sehr kurz, 3 fast doppelt so lang wie 4, 3 bis 10 fast parallel. Halsschild wie bei *repandus*; Oberfläche chagriniert. Flügeldecken wie bei *repandus*. Tergit 8 Abb. 406. Sternit 8 Abb. 407.

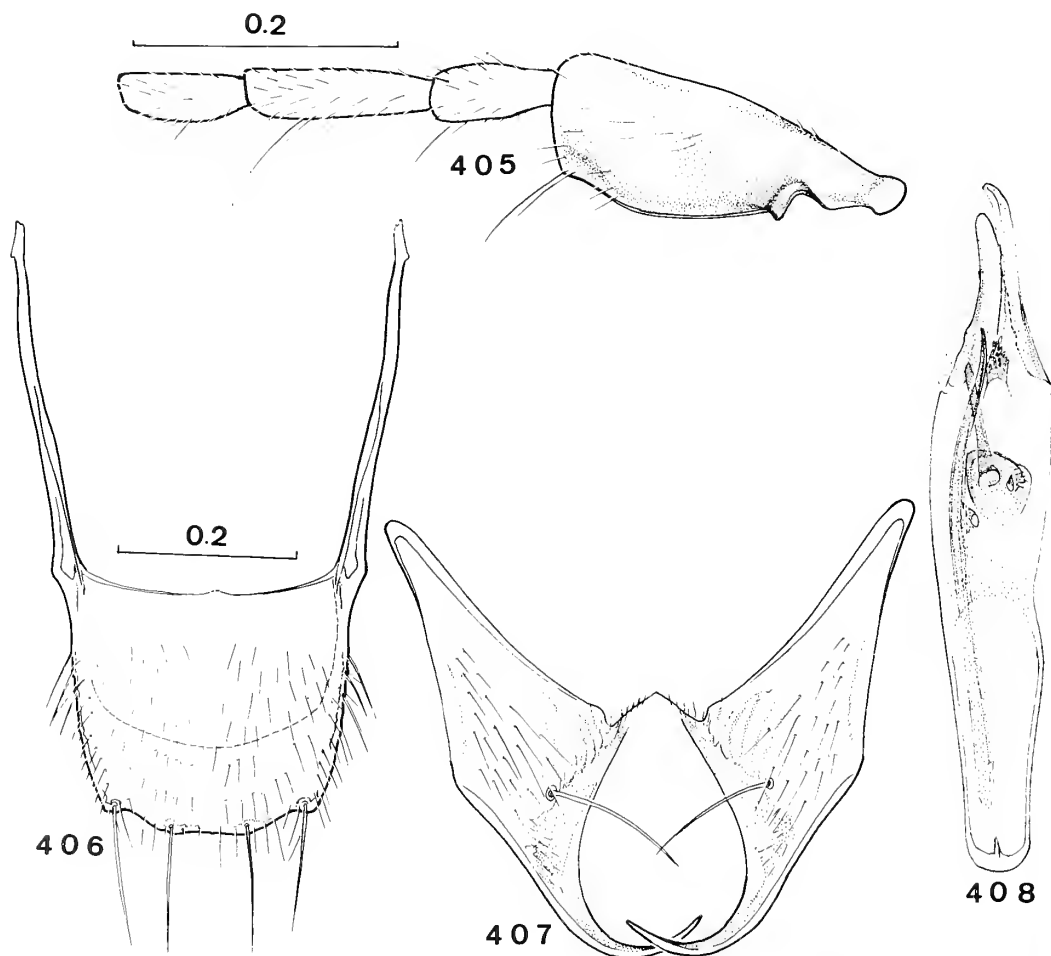


Abb. 405-408. *Sphinginopalpus* s. str. *wezaensis* sp. nov. ♂: 405, Fühlerglieder 1-4; 406, Tergit 8; 407, Sternit 8; 408, Kopulationsapparat (dorsal). Massstab von 405 auch für 407 und 406 auch für 408.

Kopulationsapparat Abb. 408 dorsal.

Holotypus (TMP): South Africa, SW Natal: Weza indigen. forest, grassnetting, 30°35'S, 29°45'E, 24.ii.1985, E-Y:2160, S. Endrödy-Younga.

Die neue Art ist neben *leucosideae* Wittmer zu stellen, doch ist das Fühlerglied 1 weniger parallel und die Terminalia verschieden.

66. *Sphinginopalpus* s. str. *dentatus* sp. nov.

MÄNNCHEN (Abb. 409-415).

Länge 2 mm.



409

410

Abb. 409-410. *Sphinginopalpus* s. str. *dentatus* sp. nov. ♂: 409-410, Maxillarpalpen (x170) (409, von oben; 410, von unten).

Oberfläche glatt. Maxillarpalpen Abb. 409-410. Fühler (Abb. 411) um ca. 1/5 kürzer als die Flügeldecken, Glied 3 deutlich länger als 4 (von der Abbildung leider nicht ersichtlich). Halsschild länger als breit (17x14), Seiten nach vorne nur schwach verengt, fast parallel; sonst wie *elongatidens*, Flügeldecken langoval; falsche Epipleuren ca. 70% der Länge einnehmend, Krenulierung angedeutet; Punkte in Reihen bis über die Mitte gross, dann verworren und praktisch erlöschend. Tergit 8 Abb. 412. Sternite 7 und 8 Abb. 413 und 414.

Kopulationsapparat Abb. 415 dorsal.

Holotypus (TMP): South Africa, N Transvaal: Soutpansberg, Hanglip, grassnetting summit, 30°00'S, 29°54'E, 18.iii.1973, E-Y:68, S. Endrödy-Younga.

Der lange Zahn auf Fühlerglied 1 erinnert an *curvispinus* Wittmer und *acutispinus* Wittmer, neben die die neue Art zu stellen ist, doch sind die Maxillarpalpen und die Terminalia verschieden gebaut.

Kopf schwarz, Vorderkopf gelb ohne die Augen und die Wangen zu erreichen; Maxillarpalpen dunkelbraun, stellenweise leicht aufgehellte; Fühler schwarz, die ersten 5 Glieder gelb; Halsschild schwarz, abgeflachte Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit einem gelblichweissen Seitensaum, sofort hinter den Schultern beginnend und die Spitzen fast erreichend; Hinterbeine schwarz, Hintertarsen schwach aufgehellte, 4 vordere Schenkel dunkelbraun, 4 vordere Tibien und Tarsen gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt;

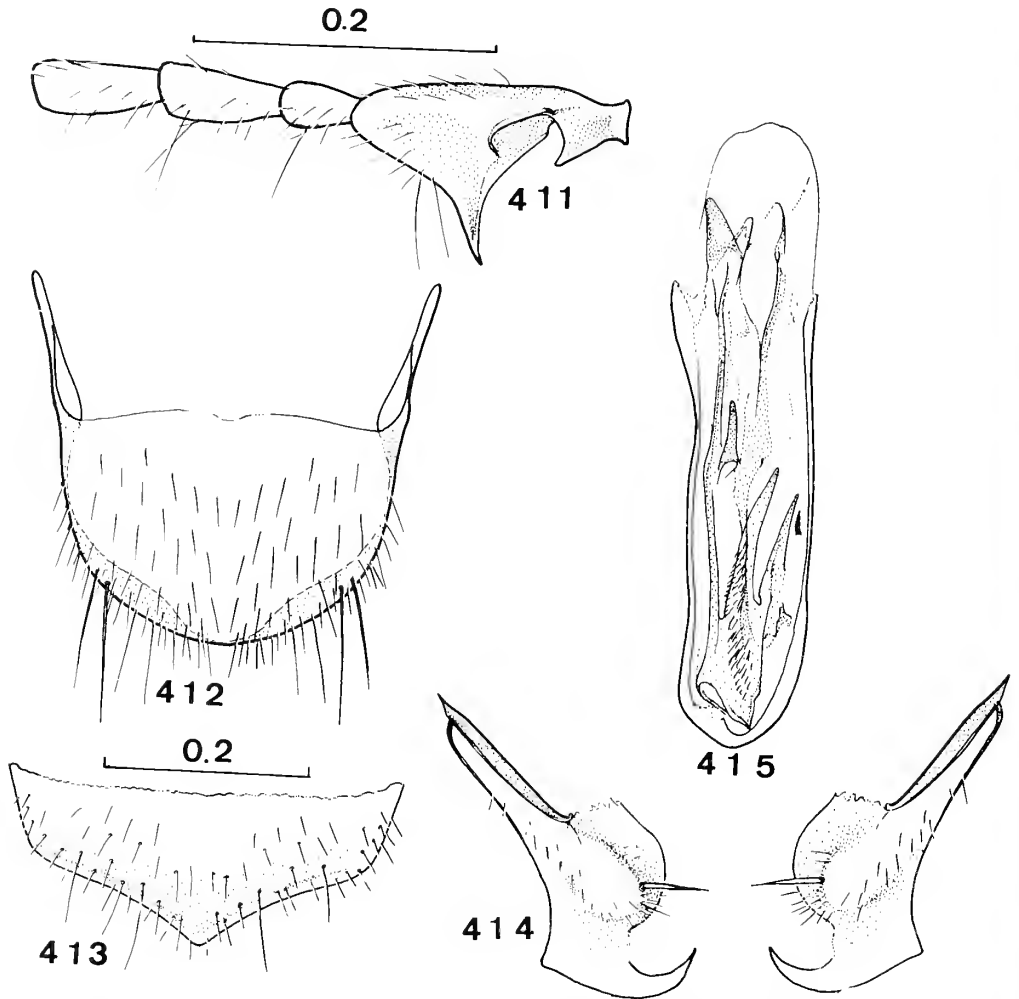


Abb. 411-415. *Sphinginalpalpus* s. str. *dentatus* sp. nov. ♂: 411, Fühlerglieder 1-4; 412, Tergit 8; 413, Sternit 7; 414, Sternit 8; 415, Kopulationsapparat (dorsal). Massstab von 411 auch für 412, 414, 415.

67. *Sphinginalpalpus* s. str. *bedfordensis* sp. nov.

MÄNNCHEN (Abb. 416-421).

Länge 2 mm.

Kopf einfarbig schwarz, oder mit einem kleinen, gelblichen Flecken auf dem Vorderkopf, zwischen den Fühlerwurzeln, die Augen und Wangen nicht erreichend; Maxillarpalpen dunkelbraun; Fühler schwarz, Glieder 1 bis 4 gelb oder aufgehellt, 1 an der Basis, 2 an der Spitze, 3 an der Basis

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

schwärzlich; Halsschildschwarz, abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit weisslichgelben Seiten, beginnend unter den Schultern bis zu den Spitzen, vor der Mitte kurz und undeutlich ein wenig nach innen erweitert; Hinterbeine schwarz, Hintertibien wenig, Hintertarsen ein wenig stärker aufgehellte, 4 vordere Schenkel dunkel mit aufgehellten Knien, 4 Vordertibien und 4 Vordertarsen gelb.



416



417

Abb. 416-417. *Sphinginopalpus* s. str. *bedfordensis* sp. nov. ♂: 416-417, Maxillarpalpen (x220) (416, von oben; 417, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 416-417. Fühler (Abb. 418) um ca. 1/4 kürzer als die Flügeldecken, Glied 3 ein wenig länger als 4. Halsschild nur wenig länger als breit (19x18); Sonst wie bei *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 80% der Länge einnehmend, nicht krenuliert; Punktreihen regelmässig, bis über die Mitte deutlich, dann Punkte spärlicher, fast erlöschend. Tergit 8 Abb. 419. Sternit 8 Abb. 420.

Kopulationsapparat Abb. 421 dorsal.

WEIBCHEN.

Kopf einfarbig schwarz, sonst wie das ♂ gefärbt.

Holotypus und 9 Paratypen (NHMB): South Africa, Cape Prov.: 5-14 km S Bedford (Karoo), 600/730m, 11.x.1984, W. Wittmer. S Transvaal: Robertsdrift, Vaal R., from flood debris, 8.x.1973, 27°02'S, 29°02'E, E-Y:189, S. Endrödy-Younga, 13 Paratypen (TMP), 4 Paratypen (NHMB), 2 Paratypen (AMG).

Eine kleine Art die dem *oneili* Pic nahesteht, mit ähnlich gebauten Maxillarpalpen, Fühlerglied 1 und Terminalia sehr verschieden.

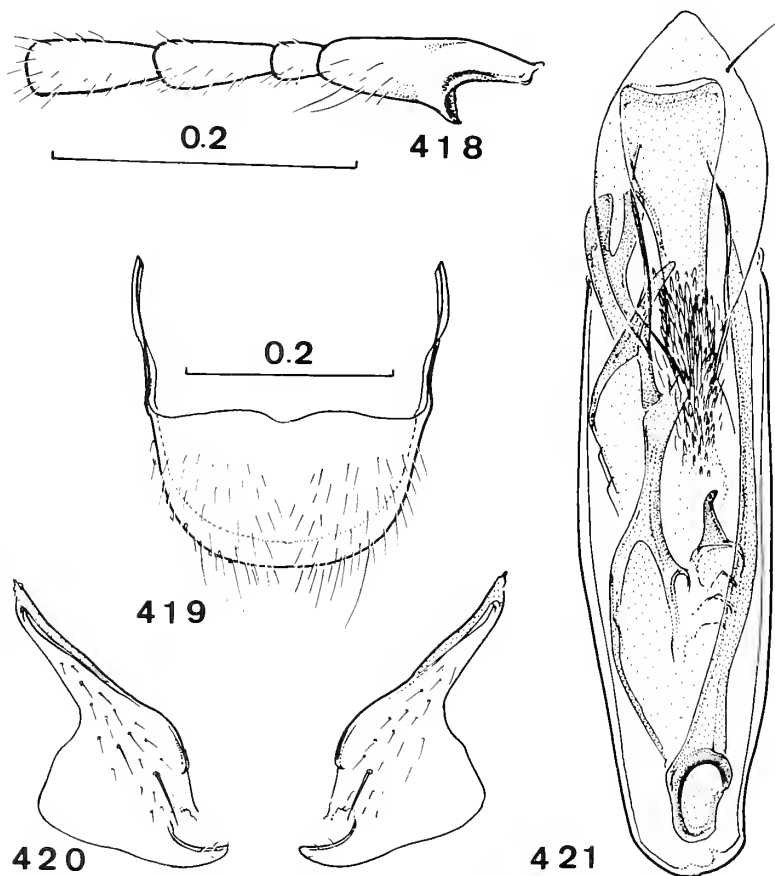


Abb. 418-421. *Sphinginopalpus* s. str. *bedfordensis* sp. nov. ♂: 418, Fühlerglieder 1-4; 419, Tergit 8; 420, Sternit 8; 421, Kopulationsapparat (dorsal). Massstab von 418 auch für 420, 421.

68. *Sphinginopalpus* s. str. *zimbabwensis* sp. nov.

Sphinginopalpus albilabris (Boheman) - Champion, 1922: 332 parte.

MÄNNCHEN (Abb. 422-427).

Länge 1,8 mm.

Diese Art die von Champion, 1922, zu *albilabris* gestellt wurde, stellte sich als neu heraus.

Kopf schwarz, von der Mitte der Augen nach vorne mit den Wangen gelb; Maxillarpalpen gelb; Fühler gelb, letzte 3 bis 4 Glieder ein wenig angedunkelt; Halsschild schwarz, abgeflachter Teil gelborange; Schildchen und Flügeldecken schwarz, letztere mit ziemlich kurzen, gelblichweissen Seiten, die die Länge und Breite der falschen Epipleuren einnehmen; Schenkel schwarz, die vorderen

DIE GATTUNG *SPHINGINOPALPUS* PIC (COLEOPTERA: MALACHIIDAE)

und mittleren gegen die Knie aufgehehlt, Tibien und Tarsen gelb, die hinteren angedunkelt.

Gestalt und Färbung wie *majeri* Wittmer. Maxillarpalpen Abb. 422- 423. Fühlerglieder 1 bis 4 Abb. 424. Tergit 8 Abb. 425. Sternit 8 Abb. 426.

Kopulationsapparat Abb. 427 dorsal.

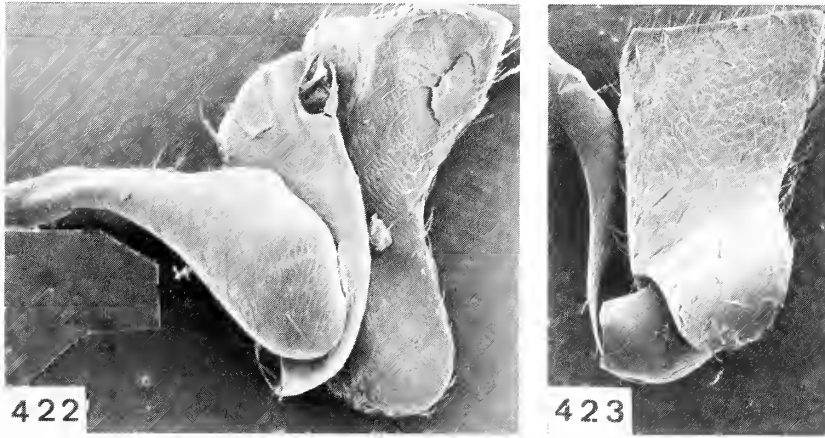


Abb. 422-423. *Sphinginopalpus* s. str. *zimbabwensis* sp. nov. ♂: 422-423, Maxillarpalpen (x200)
(422, von oben; 423, von unten).

Holotypus (BM): Zimbabwe (Mashonaland): Salisbury (Harare), iii.1895, G. A. K. Marshall.

Diese neue Art ist näher mit *majeri* Wittmer als mit *albilabris* (Boheman) verwandt, sie hat einen ähnlich langen Halsschild, doch ist sie durch die verschieden gebauten Terminalia und das Fühlerglied 1 leicht zu unterscheiden.

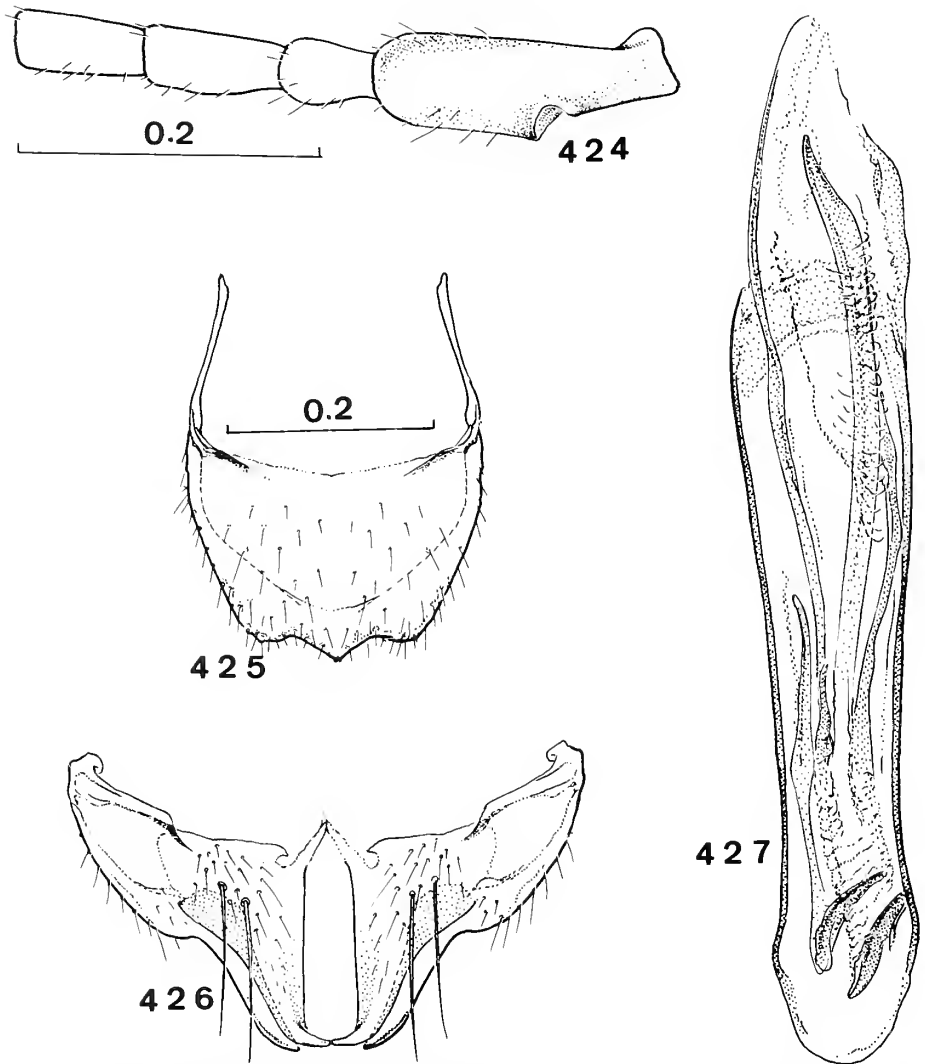


Abb. 424-427. *Sphinginopalpus* s. str. *zimbabwensis* sp. nov. ♂: 424, Fühlerglieder 1-4; 425, Tergit 8; 426, Sternit 8; 427, Kopulationsapparat (dorsal). Massstab von 424 auch für 426, 427.

69. *Sphinginopalpus* s. str. *basutolandicus* sp. nov.

MÄNNCHEN (Abb. 428-433).

Länge knapp 2 mm.

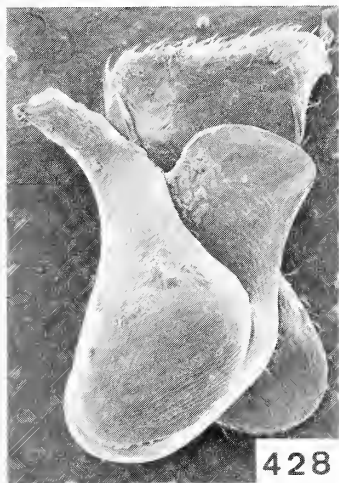


Abb. 428-429. *Sphinginopalpus* s. str. *basutolandicus* sp. nov. ♂: 428-429, Maxillarpalpen (x200) (428, von oben; 429, von unten).

Kopf mit den Wangen einfarbig schwarz; Fühler gelbbraun, Basis von Glied 1 schwarz, Spitze von 2 und 3 fast ganz dunkel; Halsschild schwarzbraun, fast ganze abgeflachte Basis gelblich aufgehell; Schildchen und Flügeldecken schwärzlich, Seiten der letzteren von der Basis bis zu den Spitzen gelblich, vor der Mitte ist die helle Färbung schmal und verschwommen gegen die Naht ausgedehnt; Schienen und Tarsen, besonders die 4 vorderen vorwiegend gelblich, Schenkel fast schwarz.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 428-429. Fühler (Abb. 430) um 1/5 kürzer als die Flügeldecken, Glied 3 deutlich länger und ein wenig breiter als 4. Halsschild ein wenig länger als breit (14,5x13,5), Oberfläche glatt. Flügeldecken langoval, Schulterbeulen gut entwickelt; falsche Epipleuren ca. 80% der Länge einnehmend, nicht krenuliert; Oberfläche glatt, Punktreihen bis über die Mitte deutlich, dann Punkte an Tiefe verlierend, verworren, spärlich. Tergit 8 Abb. 431. Sternit 8 Abb. 432.

Kopulationsapparat Abb. 433 dorsal.

Holotypus (ZML), 1 Paratypus (NHMB): South Africa, Basutoland: Nazareth M. S. 20 miles ESE Maseru, 24.iii.1951 (No. 245), Swedish South Africa Expedition 1950-1951, Brinck, Rudebeck.

Diese neue Art ist neben *bedfordensis* Wittmer zu stellen, von der sie sich durch Fühlerglied 1, das verdickte Glied 3 und das verschieden gebaute Sternum 8 unterscheidet, das am Innenrand mit 2 langen Borsten bewehrt ist, *bedfordensis* hat nur eine Borste; der Kopulationsapparat zeigt weniger Unterschiede.

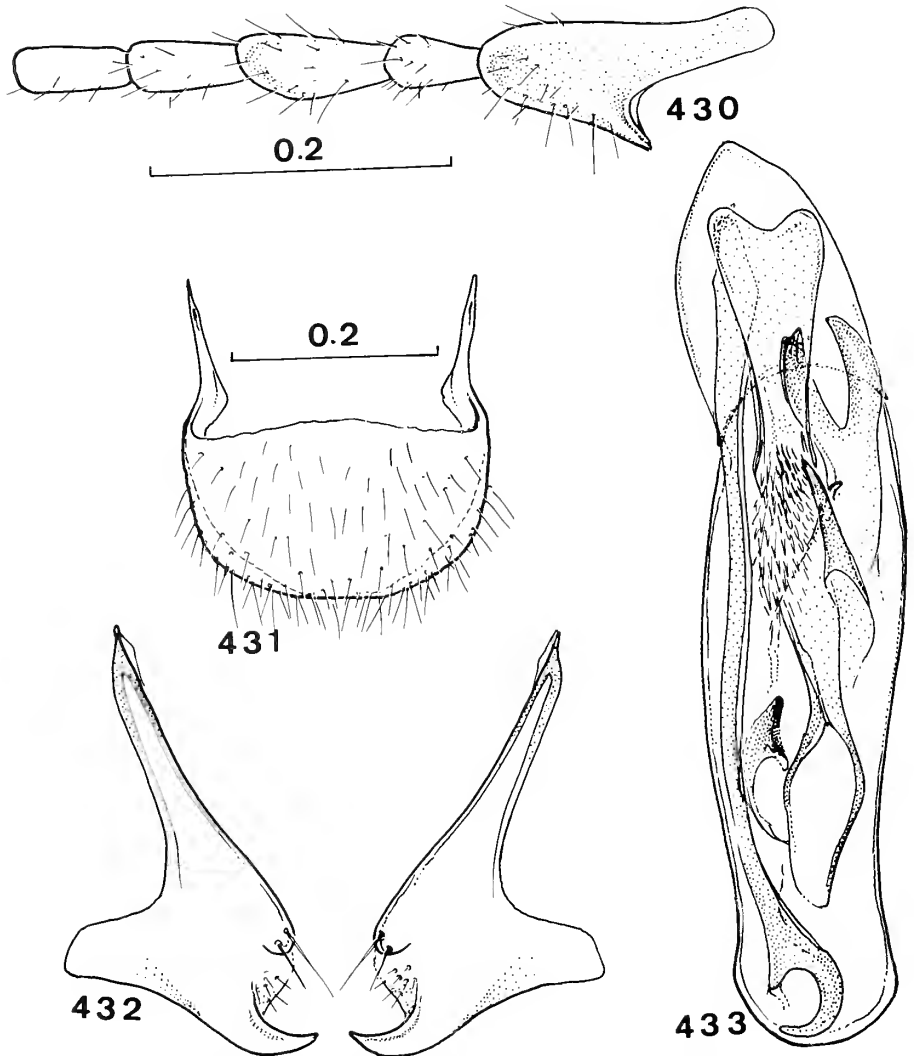


Abb. 430-433. *Sphinginopalpus* s. str. *basutolandicus* sp. nov. ♂: 430, Fühlerglieder 1-5; 431, Tergit 8; 432, Sternit 8; 433, Kopulationsapparat (dorsal). Massstab von 430 auch für 432, 433.

70. *Sphinginopalpus* s. str. *breytenbachae* sp. nov.

MÄNNCHEN (Abb. 434-439).

Länge 2,2 mm.

Kopf schwarz, ein kleiner verschwommener Flecken auf dem Vorderkopf zwischen und über den Fühlerwurzeln und Wangen gelb, ein schmaler Fortsatz auf die Stirne bis zur Mitte der Augen verlängert. Maxillarpalpen schwärzlich, teils bräunlich aufgehellte; Fühler gelb, letzte 5 Glieder, sowie Basis von 1, schwärzlich; Halsschild schwarz, Basis schmal, kaum aufgehellte; Schildchen und Flügeldecken schwarz, letztere jederseits mit einem weisslichen, antimedialen, dreieckigen Flecken, der fast bis zur Naht reicht; Hinterbeine schwarz, Hintertarsen etwas aufgehellte, 4 Vorderschenkel dunkel, an den Knien kurz hell, 4 Vordertibien gelb, an der Basis dunkel, 4 Vordertarsen gelb, letztes Glied leicht dunkler.

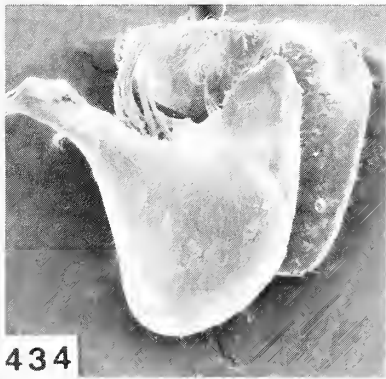


Abb. 434-435. *Sphinginopalpus* s. str. *breytenbachae* sp. nov. ♂: 434-435, Maxillarpalpen (x170) (434, von oben; 435, von unten).

Krenulierung nur stellenweise kaum angedeutet; Punktreihen anfangs regelmässig, nach hinten aufgelöst, Punkte erlöschend. Tergit 8 Abb. 437. Sternit 8 Abb. 438.

Kopulationsapparat Abb. 439 dorsal.

Holotypus (TMP): South Africa, N Karoo: Baviaankloof, beating, 33°38'S, 24°26'E, 13.i.1979, W-B., W. Breytenbach.

Eine neue Art mit tief ausgehöhltem Fühlerglied 1 an der Basis mit schwach stumpfem Zahn, ausserdem gekennzeichnet durch das in der Mitte kurz, ziemlich tief ausgerandete Tergit 8.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen Abb. 434-435. Fühler (Abb. 436) um ca. 1/4 kürzer als die Flügeldecken, Glied 3 kaum merklich länger als 4. Halsschild länger als breit (16x14), Oberfläche glatt, abgeflachter Teil chagriniert, sonst wie bei *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 55% der Länge einnehmend,

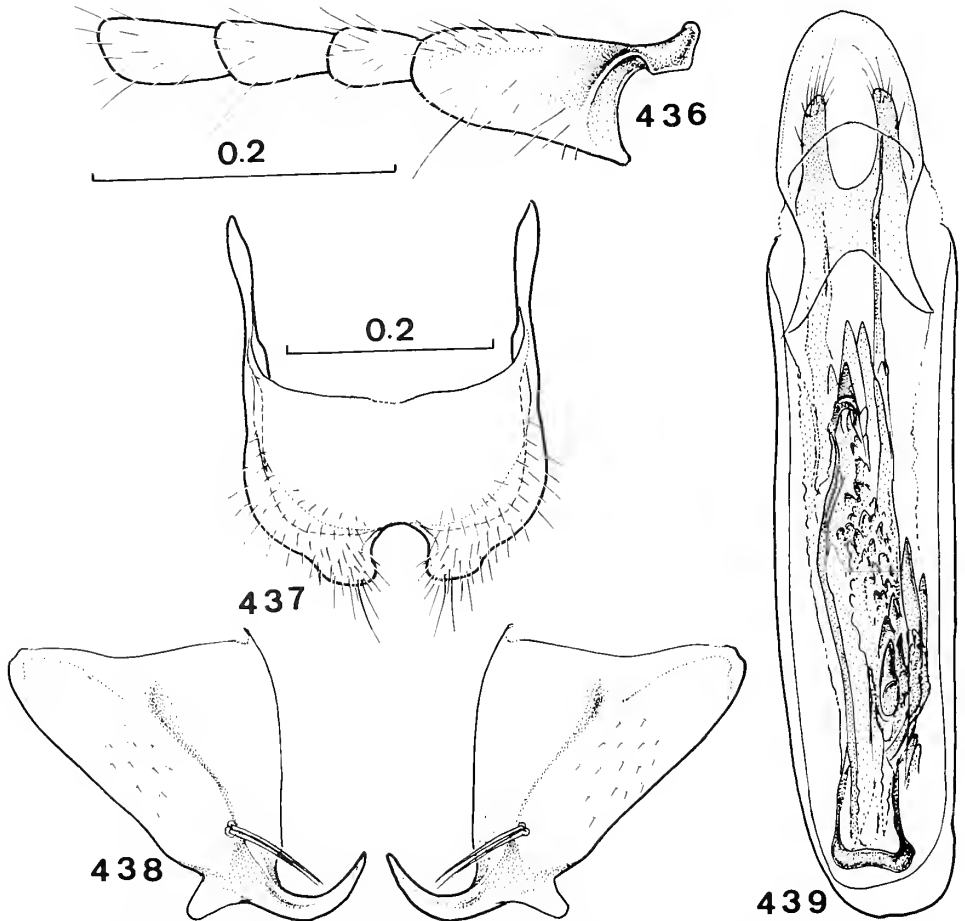


Abb. 436-439. *Sphinginalpalpus* s. str. *breytenbachae* sp. nov. ♂: 436, Fühlerglieder 1-4; 437, Tergit 8; 438, Sternit 8; 439, Kopulationsapparat (dorsal). Massstab von 436 auch für 438, 439.

71. *Sphinginalpalpus* s. str. *elongatidens* sp. nov.

MÄNNCHEN (Abb. 440-445).

Länge 2,5 mm.

Kopf mit den Wangen schwarz, Vorderkopf beginnend von der Mitte der Augen, gelb; Maxillarpalpen dunkel, letztes Glied, besonders an der Spitze aufgehell; Fühler schwärzlich, Glieder 1 bis 4 gelb; Halsschild schwarz, die ganze abgeflachte Basis hellbraun; Schildchen und Flügeldecken schwarz, Seiten von der Basis bis fast zu den Spitzen schmal gelb, Spitzen kurz, schwach aufgehell, antimediane gelbe Quermakel an der Naht unterbrochen oder durchgehend; Hinterbeine schwarz, Hintertarsen leicht aufgehell, Mittel- und Vorderschenkel schwarz, Mitteltibien etwas weniger stark

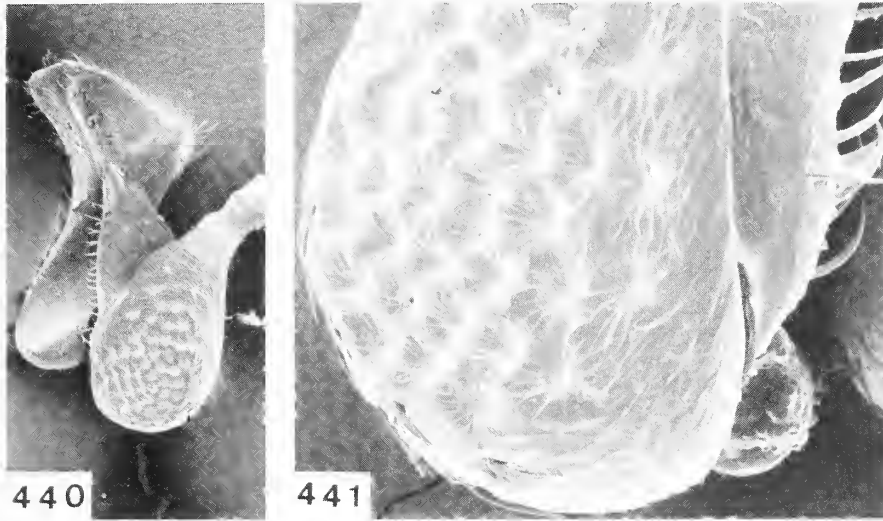


Abb. 440-441. *Sphinginopalpus* s. str. *elongatidens* sp. nov. ♂: 440-441, Maxillarpalpen (440, von oben, x130; 441, Glied 1, x 625).

aufgehellt als die vorderen, 4 Vordertarsen weitgehend gelb.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen (Abb. 440-441), Glied 1 auf der Oberseite mit ziemlich tiefen und breiten Gruben bedeckt, ähnlich wie bei *tridens* (Abb. 456). Fühler (Abb. 442) verhältnismässig kurz, fast um 1/3 kürzer als die Flügeldecken, Glied 1 durch einen sehr langen, allmählich verschmälerten, leicht verdrehten Fortsatz ausgezeichnet, der fast in der Mitte des Gliedes steht, auf der Höhe der Ausrandung steht eine kurze, quere Lamelle, 3 und 4 ungefähr gleich lang. Halsschild länger als breit (17x15,5), in der Mitte am breitesten, Seiten nach vorne schwach gerundet verengt, gegen die Basis eingeschnürt; Seitenrand die Basis nicht ganz erreichend, Basalrand deutlich; Oberfläche glatt, an den Seiten der abgeflachten Basis chagriniert. Flügeldecken langoval, Schulterbeulen normal, falsche Epipleuren lang, ca. 80% der Länge einnehmend, nicht krenuliert; Oberfläche glatt, auf dem basalen Teil mit ca. 6 Punktreihen, die an den Seiten weniger deutlich sind, auf dem hinteren Teil Punkte verworren. Tergit 8 Abb. 443. Sternit 8 Abb. 444.

Kopulationsapparat Abb. 445 dorsal.

Holotypus (TMP): South Africa, E Transvaal: Nelshoogte Forest Station, grassnetting, 25°50'S, 30°50'E, 1.xii.1986, E-Y:2335, S. Endrödy-Younga; Berlin Forest Station, grassnetting, 1500 m, 25°32'S, 30°44'E, 7.xii.1986, E-Y:2360, S. Endrödy-Younga, 3 Paratypen (TMP), 2 Paratypen (NHMB). Transkei (Pondoland): Port St. John, 7.-13.viii.1923, R. E. Turner, 1 Paratypus (BM).

Diese neue Art ist neben *curvidens* Wittmer zu stellen, sie unterscheidet sich durch das verschieden gebaute Fühlerglied 1, die Maxillarpalpen und die Terminalia. Die Gruben auf der Oberseite von Glied 1 der Maxillarpalpen sind ähnlich wie bei *tridens*.

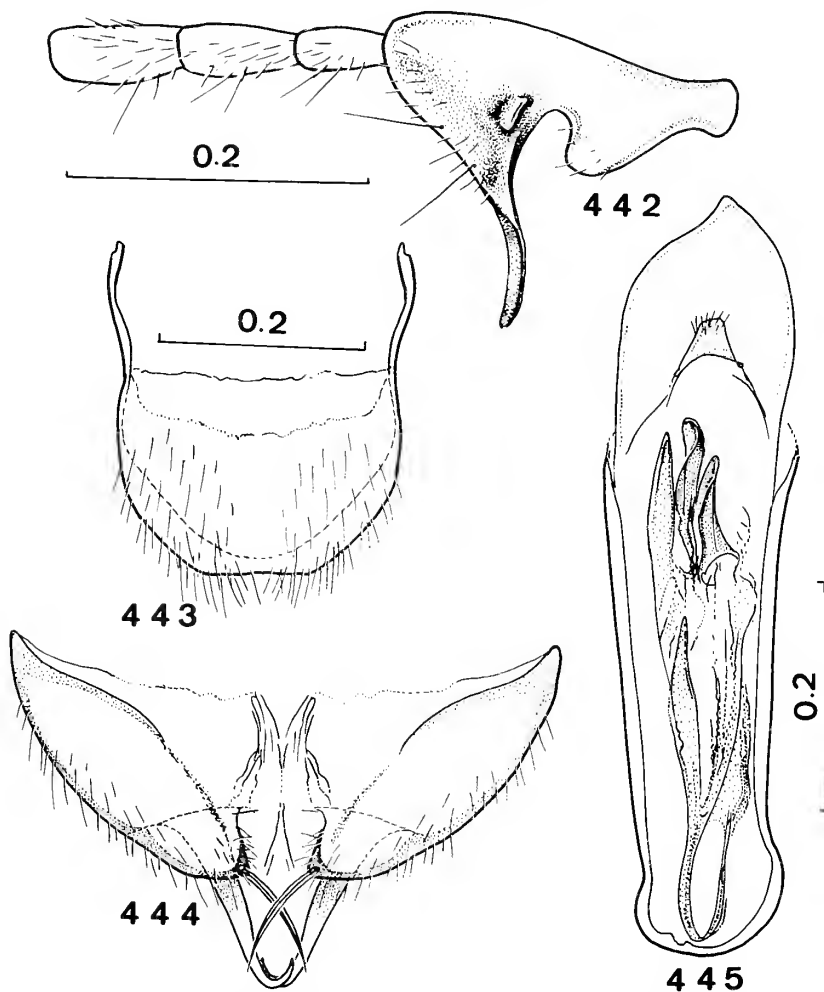


Abb. 442-445. *Sphinginopalpus* s. str. *elongatidens* sp. nov. ♂: 442, Fühlerglieder 1-4; 443, Tergit 8; 444, Stermit 8; 445, Kopulationsapparat (dorsal). Massstab von 442 auch für 444, 445.

72. *Sphinginopalpus* s. str. *karkloofensis* sp. nov.

MÄNNCHEN (Abb. 446-451).

Länge 2,2-2,3 mm.

Kopf schwarz; Glied 3 der Maxillarpalpen schwarz, leicht aufgehell; Fühler schwarz, Glieder 1 bis 3 gelb, wobei 1 beginnend an der Basis mehr oder weniger stark angedunkelt ist; Halsschild schwarz, abgeflachter Teil braun; Schildchen und Flügeldecken schwarz, letztere mit schmalen,

weissen Seiten, beginnend unter den Schulterbeulen bis fast zu den Spitzen, bei 1 Ex. mit einer antimedialen Quermakel, die etwas verschwommen ist und die Naht nicht erreicht; alle Schenkel schwarz, Tibien und Tarsen gelb, oder die hinteren leicht angedunkelt.

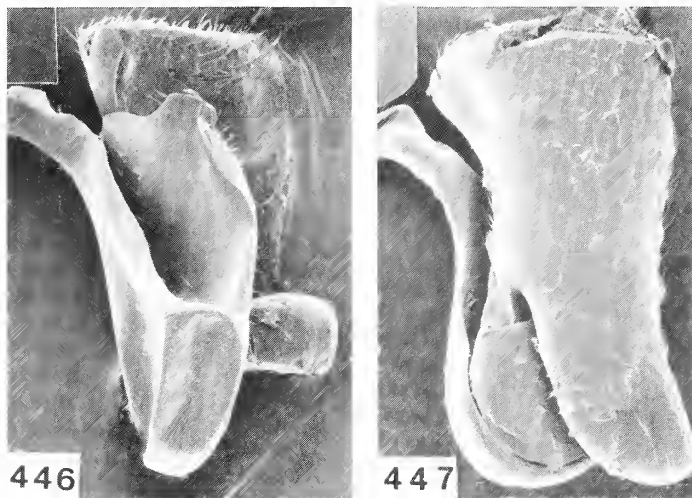


Abb. 446-447. *Sphinginopalpus* s. str. *karkloofensis* sp. nov. ♂: 446-447, Maxillarpalpen (x170) (446, von oben, 447, von unten).

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt mit feinen Punkten, die auf der vorderen Hälfte deutlicher sind. Maxillarpalpen Abb. 446-447. Fühler (Abb. 448) um ca. 1/4 kürzer als die Flügeldecken, Glied 3 nur wenig länger als 4, 4 ein wenig breiter als 5. Halsschild länger als breit (16x15), sonst wie bei *elongatidens*, jedoch Oberfläche variabel, beim Exemplar von Karkloof fast ganz glatt, beim anderen von Isidenge auf der abgeflachten Stelle weitgehend chagriniert. Flügeldecken langoval, wie bei *elongatidens*, Punktreihen etwas deutlicher, weiter nach hinten reichend, falsche Epipleuren lang, kaum merklich krenuliert, fast glatt. Tergit 8 Abb. 449. Sternit 8 Abb. 450.

Kopulationsapparat Abb. 451 dorsal.

Holotypus (TMP): Natal: Karkloof grassveld with river, 29°19'S, 30°15'E, 7.xii.1989, E-Y:2747, S. Endrödy-Younga. Cape Prov.: Isidenge Forest Station, 32°41'S, 27°15'E, 18.xi.1987, E-Y:2522, grassnetting and Arum fl., S. Endrödy-Younga, 1 Paratypus (NHMB).

Diese neue Art ist auffällig durch ihr fast dreieckiges Fühlerglied 1, das an der Basis tief ausgerandet ist, die Terminalia und hier besonders das Sternit 8 sind sehr charakteristisch.

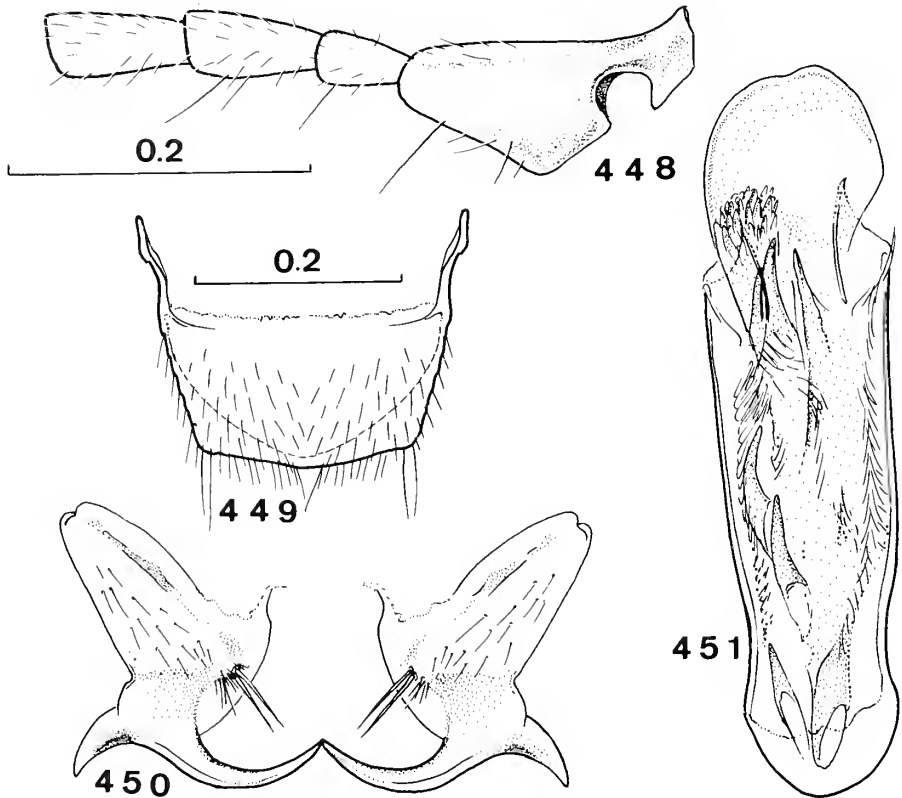


Abb. 448-451. *Sphinginopalpus* s. str. *karkloofensis* sp. nov. ♂: 448, Fühlerglieder 1-4; 449, Tergit 8; 450, Sternit 8; 451, Kopulationsapparat (dorsal). Massstab von 448 auch für 450, 451.

73. *Sphinginopalpus* s. str. *nylsvleyensis* sp. nov.

MÄNNCHEN (Abb. 452-456).

Länge 1,8-2 mm.

Kopf schwarz, von der Mitte der Augen nach vorne inklusive der Wangen gelb; Maxillarpalpen braun bis dunkelbraun; Fühler schwärzlich, erste 4 bis 5 Glieder gelb; Halsschild schwarz, abgeflachter Teil gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit langem gelbem Seitenband, das antimedial ein wenig verbreitert ist; Hinterschenkel schwarz, mittlere Schenkel ebenso, gegen die Knie aufgehellt, Mitteltibien und Mitteltarsen gelb (übrige Tarsen fehlen).

Kopf mit den Augen nur ganz wenig breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt mit feinen zerstreuten Haarpunkten. Maxillarpalpus Abb. 452. Fühler (Abb. 453) um 1/4 kürzer als die Flügeldecken, Glied 3 nur ein wenig länger als 4. Halsschild länger als breit (15,5x14), sonst wie bei *elongatidens*. Flügeldecken langoval; falsche Epipleuren ca. 60% der Länge einnehmend, keine Krenulierung; Punktreihen regelmässig, Punkte weit auseinander stehend. Tergit 8 Abb. 454.



Abb. 452. *Sphinginopalpus* s. str. *nylsvleyensis* sp. nov. ♂: 452, Maxillarpalpus (x220, von oben).

Sternit 8 Abb. 455.

Kopulationsapparat Abb. 456 dorsal.

Holotypus (TMP): South Africa, N Transvaal: Nylsvley, at river, ground trap with banana bait, replication 4, 24°40'S, 28°42'E, 3.ix.1975, E-Y:875, S. Endrödy-Younga; Roberts Drift, Vaal R., from flood debris, 27°02'S, 29°02'E, 8.x.1973, E-Y:189, S. Endrödy-Younga, 1 Paratypus (TMP), 1 Paratypus (NHMB).

Eine kleine Art, die neben *dwesaensis* Wittmer zu stellen ist, mit ähnlich gebautem Fühlerglied 1, jedoch sehr verschiedenen Terminalia.

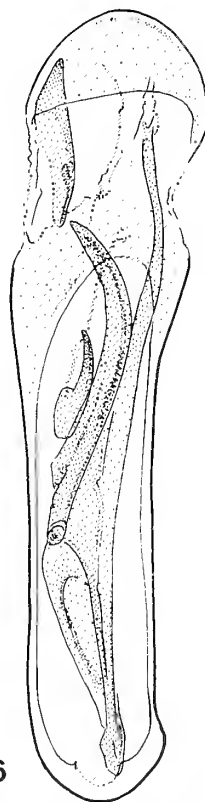
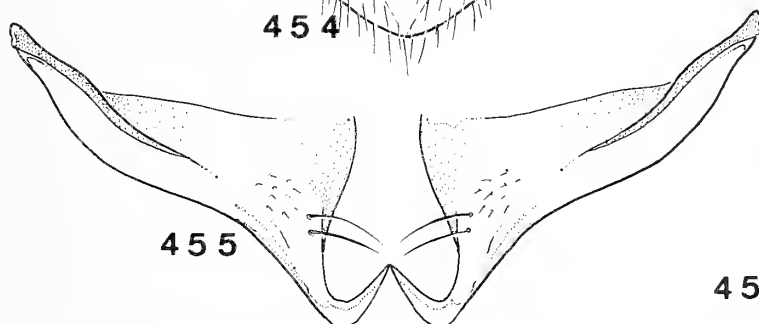
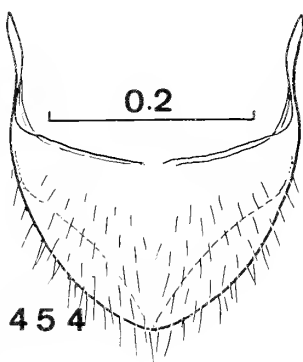
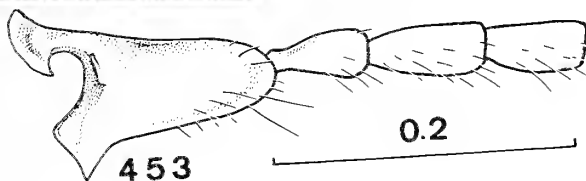


Abb. 453-456. *Sphinginopalpus* s. str. *nylsvleyensis* sp. nov. ♂: 453, Fühlerglieder 1-4, 454, Tergit 8; 455, Sternit 8; 456, Kopulationsapparat (dorsal). Massstab von 452 auch für 455, 456.

74. *Sphinginopalpus s. str. tridens* sp. nov.

MÄNNCHEN (Abb. 457-461).

Länge 2 mm.

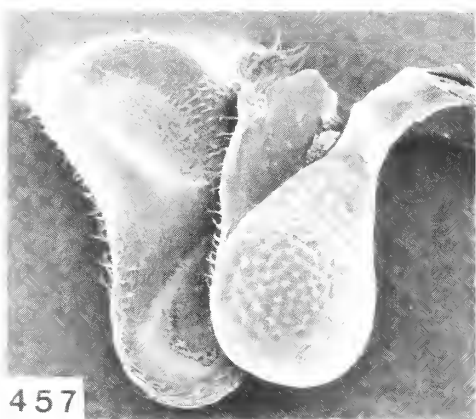


Abb. 457. *Sphinginopalpus s. str. tridens* sp. nov. ♂:
457, Maxillarpalpus (x170, von oben).

Kopf schwarz, Wangen um die Fühlerwurzeln, verbunden mit einer schmalen Verlängerung bis zur Mitte der Augen und ein kleiner Flecken über den Fühlerwurzeln, gelblich; Maxillarpalpen gelbbraun; Fühler schwärzlich, die ersten 5 Glieder gelb; Halsschild schwarz, abgeflachter Teil an der Basis gelbbraun; Schildchen und Flügeldecken schwarz, letztere mit schmalen gelben Seiten, unter den Schultern beginnend und fast die Spitzen erreichend, antimedial gegen die Naht verbreitert, ohne sie zu erreichen; Schenkel schwarz, die vorderen gegen die Knie aufgeheilt, Schienen und Tarsen gelb, die hinteren leicht angedunkelt.

Kopf mit den Augen breiter als der Halsschild, Stirne leicht gewölbt; Oberfläche glatt. Maxillarpalpen (Abb. 457) haben auf der Oberseite von Glied 1 ziemlich tiefe und breite Gruben, ähnlich

wie bei *elongatidens* (Abb. 439-440). Fühler (Abb. 458) um 1/4 kürzer als die Flügeldecken, Glied 3 kaum merklich länger als 4. Halsschild so lang wie breit, sonst wie bei *elongatidens*. Flügeldecken langoval, falsche Epipleuren ca. 80% der Länge einnehmend, Krenulierung fehlt; Punktierung viel weniger dicht als bei *elongatidens* und weniger deutlich in Längsreihen angeordnet. Tergit 8 Abb. 459. Sternit 8 Abb. 460.

Kopulationsapparat Abb. 461 dorsal.

Holotypus und 1 Paratypus (TMP), 1 Paratypus (NHMB): South Africa, Natal Middld.: Karkloof grassveld, 29°19'S, 30°15'E, 7.xii.1989, E-Y:2737, 2747, S. Endrödy-Younga, I. Klimaszewski.

Diese neue Art ist neben *elongatidens* Wittmer zu stellen, Fühler von ähnlicher Bauart, Maxillarpalpen, Terminalia und Kopulationsapparat sehr verschieden.

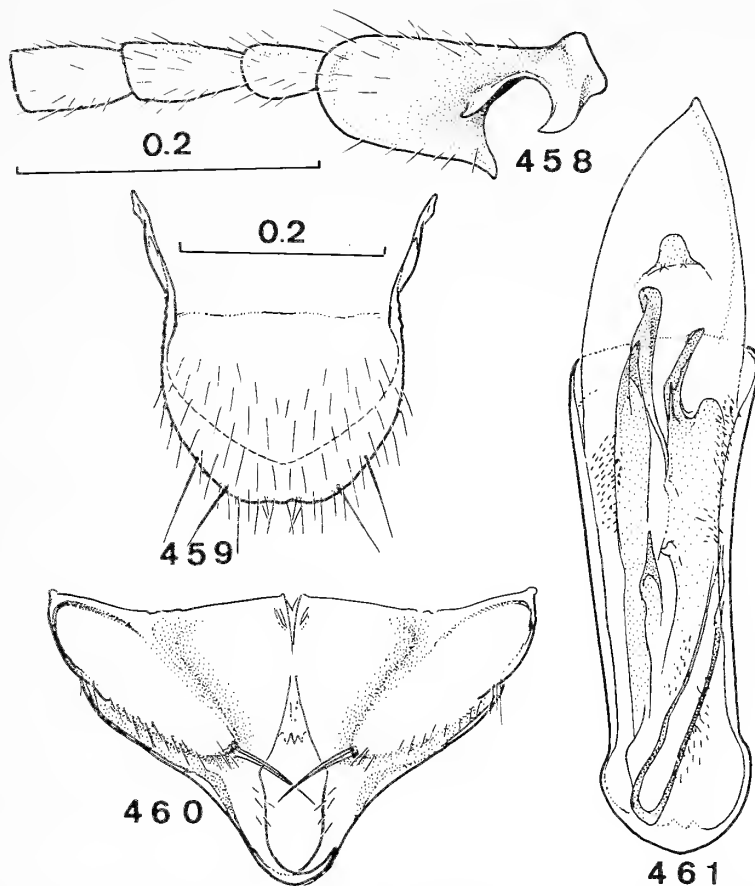


Abb. 458-461. *Sphinginopalpus* s. str. *tridens* sp. nov. ♂: 458, Fühlerglieder 1-4; 459, Tergit 8; 460, Sternit 8; 461, Kopulationsapparat (dorsal). Massstab von 458 auch für 460, 461.

LITERATUR

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Seasonal occurrence and distribution of nuptial tubercles in two African minnows, *Pseudobarbus afer* (Peters, 1864) inhabiting clear water and *Pseudobarbus asper* (Boulenger, 1911) inhabiting turbid water (Cypriniformes, Cyprinidae).

by

J. A. CAMBRAY

(Albany Museum, Grahamstown, 6140, South Africa)

ABSTRACT

Pseudobarbus afer (Peters, 1864) and *P. asper* (Boulenger, 1911) are a sister species pair which inhabit different sections of the Gamtoos River system. *Pseudobarbus afer* occurs in the clear mountain streams of the Cape Fold Belt and *P. asper* in the turbid Karoo section of the river system. The seasonal occurrence and disappearance of tubercles for both species followed the reproductive cycle and was probably under seasonal hormonal control. *Pseudobarbus afer* males had the more numerous and larger tubercles when compared to *P. asper* males. It is suggested that the enlarged, white head tubercles of *P. afer* were used for display prior to breeding, whereas during breeding the tubercles on the scales and fin rays and the larger pectoral fins were used for maintaining contact with females in the riffle spawning habitats. The relatively smaller number and size of the head tubercles on *P. asper* males possibly indicated that in turbid waters visual characters have less of a selective advantage than in clear mountain streams. The smaller number and size of tubercles on *P. asper* males would have required less resources. The remainder of the resources would then be available for other reproductive activities. *Pseudobarbus afer* and *P. asper* males had larger definitive head tubercles than the rudimentary tubercles observed on the females. Only the large females of both species had head tubercles which were never definitive and their presence on reproductively active females was difficult to explain. The lack of tubercles on the smaller females indicated the expected trade-off constraint with the energy diverted to egg production rather than sexually dimorphic characters. The smaller pectoral fins of the females, which had few if any tubercles, also indicated that it was more beneficial for the female to put reproductive effort into progeny. The development of secondary sexual characteristics of *P. afer* and *P. asper* (epidermal tubercles, breeding coloration and larger pectoral fins) is favoured on the males because the sexual characteristics all require resources which must be diverted away from growth, survival requirements and the production of gametes.

INTRODUCTION

Epidermal breeding tubercles are temporary, roughened structures which have evolved in primitive euteleostean fishes and have been recorded in at least 25 families of bony fishes in 7 orders (Wiley and Collette, 1970). In addition tubercles occur in some species of the Coregonidae, Thymallidae (Salmoniformes) and Gadidae (Gadiformes) (Kratt and Smith, 1978; Vladykov *et al.*, 1985; Witkowski, 1982 in Witkowski and Rogowska, 1991). Structural differences indicate that tubercles have evolved independently in a number of fish groups (Collette, 1977). Tubercle patterns can be used to infer similarities or differences in behaviour patterns (Wiley and Collette, 1970). The head and forepart of the body of many species of the family Cyprinidae may be covered with excrescences (Breder and Rosen, 1966) and the fish may have a bright nuptial coloration during the spawning season (Banarescu and Coad, 1991). Tubercles can be valuable systematic characters in

cyprinids (Wiley and Collette, 1970; Collette, 1977). The distribution, number, size and developmental patterns of the head tubercles represent critical characters in the separation of some species (Lachner and Jenkins, 1971). Tubercles have also been considered as important evolutionary characters (Lachner and Jenkins, 1971). They might have evolved to enable spawning individuals to maintain contact in fluvial environments. Tubercles may also be used by some fish species to defend nests and territories or possibly to stimulate females to breed (Wiley and Collette, 1970; Collette, 1977).

In African cyprinids tubercles have usually been recorded in bariliine and labeine species and less so for barbina species (Howes, 1980; Reid, 1985). Skelton (1980) noted the presence, size and patterns of tubercles on 25 *Barbus* species from southern Africa. Conical tubercles occur in all seven of the flexible-rayed redfin minnows (= *Pseudobarbus*) including *P. afer* (Peters, 1864) and *P. asper* (Boulenger, 1911). In comparison to the *Barbus* species, the flexible-rayed redfin tubercle pattern consists of large tubercles and there are also tubercles on the borders of the scales which occur in regular rows (Skelton, 1980). Barnard (1943) and Jubb (1967) recorded the presence of tubercles and smaller 'pimples' on redfin minnow species in southern Africa and used the presence or absence of tubercles as a major character to separate species in southern Africa. Tubercles have been identified as important taxonomic characters in the monophyletic *Pseudobarbus* lineage (Skelton, 1980, 1988). The tubercles in the seven redfin minnow species of the genus *Pseudobarbus* have a common distribution pattern. The size and pattern of the tubercles in *P. burchelli* Smith, 1841, *P. burgi* (Boulenger, 1911), *P. afer*, *P. asper*, *P. tenuis* (Barnard, 1938) and vestigially in *P. phlegethon* (Barnard, 1938) was found to be unique for African fish and represent a very distinct synapomorphy (Skelton, 1980). The head tubercles of *P. quathlambae* (Barnard, 1938) are more numerous and smaller than in the other flexible-rayed redfins but are arranged in the same basic pattern (Skelton, 1974). As in other cyprinids the tubercles of the flexible-rayed redfin minnows are deciduous, hypertrophied, epidermal structures with a distinct keratin cap.

Data on the seasonal occurrence of breeding tubercles are usually not collected (Collette, pers. comm., October 10, 1985) but see Collette (1965). Field studies to note seasonality of tubercle formation and wear have been rare for African cyprinids. The seasonal occurrence of these structures has not been studied in any detail for *P. afer* and *P. asper*. Skelton (1974) gave a brief account of the seasonality of the tubercles for oreodaimon (*P. quathlambae*) and Cambray and Stuart (1985) noted the seasonality of the head tubercles for *P. burchelli* over a 12 month period. A SEM micrograph of a male head tubercle scar in the species *P. quathlambae* was given by Skelton (1974).

The usual seasonal sequence for breeding tubercles is their appearance at the commencement of the breeding season and just prior to the spawning season they reach their maximum extent. Following spawning the structures break off, slough, become eroded, or gradually regress. Cambray and Stuart (1985) recorded that the next season's tubercles started to erupt through the scar left from the previous season.

In the fish species chosen for the present study, *P. afer* inhabits clear, perennial, low conductivity streams and *P. asper* inhabits the turbid, intermittent, and high conductivity section of the Gamtoos River system. Therefore, if the head tubercles of the *Pseudobarbus* species were used for any visual signal, such as sex or species recognition, the clear water species (*P. afer*) should have larger and possibly more tubercles than the species inhabiting the turbid system (*P. asper*).

METHODS

COLLECTION SITES

Pseudobarbus afer were collected from the Wit River and *P. asper* from the Groot River in the

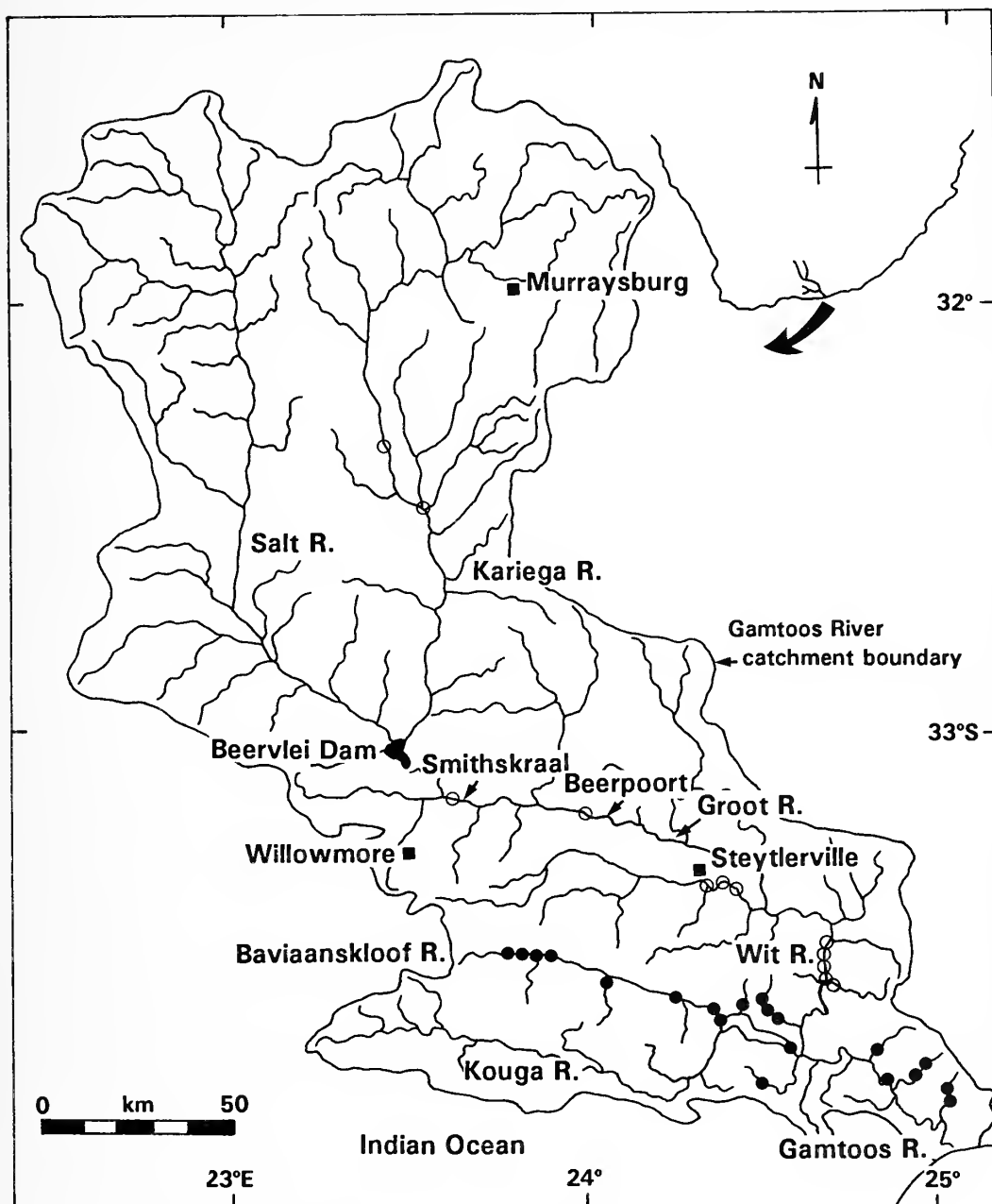


Fig. 1. Distribution of *Pseudobarbus afer* (Peters, 1864) (closed circles) and *P. asper* (Boulenger, 1911) (open circles) in the Gamtoos River system (Albany Museum records) and collection sites for the present study (Wit River for *P. afer* and Smithskraal and Beerpoort for *P. asper*).

Gamtoos River system (Fig. 1). The Gamtoos River system has two distinct catchment basins. One occurs in the Karoo where the Groot River flows over easily erodable Bokkeveld beds. The rivers are turbid, saline and intermittent (Cambray, 1992). This is the habitat of *P. asper*. The other catchment occurs within the Cape Fold Mountain Belt and is characterised by resistant quartzites. The rivers are clear, have a low conductivity and are perennial (Cambray, 1992). *Pseudobarbus afer* occur in these streams. There is no physical barrier separating these two sister species in the Gamtoos River system.

COLLECTION AND ANALYSIS

Fish were collected with a minnow seine net, fixed in 10% formalin and taken to the laboratory for analysis.

Conical tubercle formation was studied on a monthly basis for the males and females of both species over a 22 month period (July 1987 to April 1989). Fish were examined each month from a size range covering the largest fish in the sample to the smallest without any tubercles. Totals of 248 male and 118 female *P. afer* and 320 male and 157 female *P. asper* were examined (Tables 1-4). Height and basal width of the conical tubercles were measured with an eyepiece micrometer on a stereoscopic microscope (accuracy 0,05 mm). Volume of the tubercles was considered as the comparative measurement was calculated from the height and basal width data using the formula for a cone:

$$(V = \frac{\pi r^2 h}{3})$$

The terminology used by Lachner and Jenkins (1971) to describe tubercle development was followed, with several modifications. Five stages were identified, spot, bud, nuptial definitive tubercle, worn tubercle and scar. Spots were defined as distinct light areas which approach the epidermal surface. Tubercle buds were small 'pimples' which have a rounded or pointed tip. Nuptial definitive tubercles were mature structures which were hard, pointed and cornified. Worn tubercles were definitive tubercles which had lost their points and were rounded or flat but still raised above the surface. Scars were left when the tubercles were lost. Tubercles were easily distinguished from dermal sense organs simply by lifting the tubercles from the skin with a needle whereupon a small round depression would remain (Branson, 1962).

Scanning electron micrographs were taken with a JEOL Scanning Electron Microscope operating at 10 mV. Eruption and wear of tubercles were noted. Pre-spawning and post-spawning head tubercles were removed to study the microwear on the surfaces of the tubercles using standard SEM techniques. Microwear on the pectoral fin tubercles was also studied. Microwear is a term used in archaeology to describe the wear patterns on stone, bone or wooden tools caused by different uses of the tools. It was thought this method could be used to determine whether the tubercles had been used for butting females, fighting other males or for digging and making nests. It was envisaged that these activities would cause different wear patterns on the tubercles of the head and those on the pectoral fins.

The head tubercles were divided into the clusters which Skelton (1988) used to describe the pattern of tubercles in the flexible-rayed redfin minnows (Fig. 2). In each of the paired clusters the left and right sides were counted separately to see if there were different growth and/or wear patterns correlated to side. Regression analyses were run for the total number of tubercles versus standard length (SL mm) for both sexes of each species. Tests of difference of slopes of the regression lines of the total tubercle number for *P. afer* and *P. asper* males were performed by analysis of covariance (Zar, 1984). F values yielding probabilities greater than 0,95 were considered to be significant.

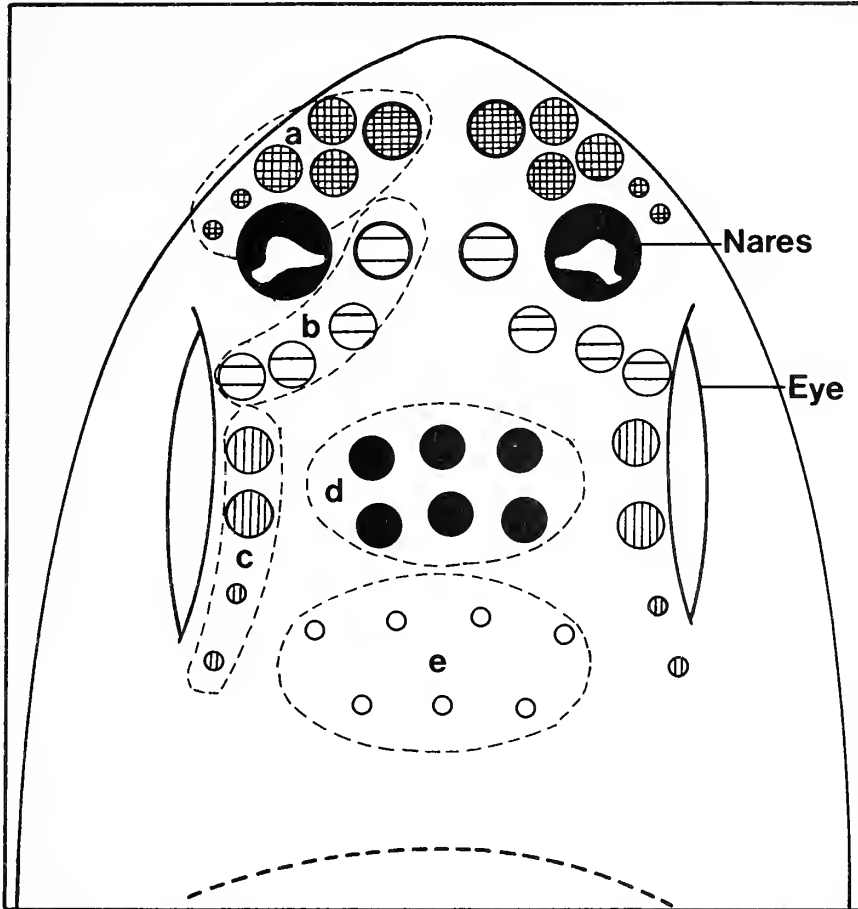


Fig. 2. Diagrammatic representation of the pattern of head tubercles on *Pseudobarbus afer* (Peters, 1864) and *P. asper* (Boulenger, 1911): (a) - cluster on snout; (b) - row above nares; (c) - row above orbit; (d) - anterior dorsal cluster; (e) - posterior dorsal cluster, (from Skelton, 1988).

Comparison of the presence or absence of definitive snout tubercles and the presence of buds on male *P. afer* and *P. asper* was graphed with the mean monthly gonadosomatic indices (data from Cambray, 1992) to show the relationship between the tubercles and increases in gonad mass. The presence of definitive tubercles was given the value 1, the presence of buds the value 0,5 and worn tubercles and scars were given the value 0.

All fins were examined for tubercle formation and presence or absence was recorded over the 22 month period of the study. The number of rows of tubercles on the rays of the pectoral fins was also recorded. This was not necessary for the other fins since there was only a single row of tubercles on each ray. Scales were examined for tubercle formation and presence or absence was recorded for the 838 fish sampled.

TABLE 1. Summary of the seasonal pattern of tubercle formation and wear in 248 *Pseudobarbus afer* (Peters, 1864) males collected over a 22 month period in the Wit River, Gamtoos River system.

Date	n	Size range SL (mm)	Tubercles ¹	Scales ²	Rays ³
Jul. 1987	11	49,2-71,1	B+Sp	-	-
Aug.	3	45,6-51,8	B+Sp	-	-
Sept.	12	39,7-62,8	D+W	+	+
Oct.	31	40,3-78,2	D+ W	+	+
Nov.	12	37,3-70,5	D+W	+	+
Dec.	8	45,9-63,4	D+W+S	+	+
Jan. 1988	7	46,0-59,2	D+W+S	-	+(few)
Feb.	12	47,2-68,1	W+S	-	+(few)
Mar.	6	42,8-63,1	W	-	+(few)
Apr.	12	39,1-66,0	W+S	-	+
May	15	43,1-65,8	W+S	-	-
June	5	46,7-58,0	B+S+Sp	-	-
July	9	51,6-72,5	B+W+S+Sp	-	-
Aug.	7	42,2-64,7	B+Sp	+(few)	-
Sept.	11	40,7-63,2	D	+	+
Oct.	12	40,6-62,5	D+W	+	+
Nov.	14	43,5-66,2	D+W+S	+	+
Dec.	5	44,2-70,1	D+W	+	+
Jan. 1989	14	37,2-69,6	B+W+S	-	+
Feb.	9	38,0-70,5	B+W	+(few)	+
Mar.	19	41,4-68,2	B+W+S	-	+
Apr.	14	38,9-67,6	B+W+S	-	+
TOTAL	248				

1. B = bud; D = definitive; S = scars; Sp = spots; W = worn

2. - = absent; + = present

3. - = absent; + = present

RESULTS

Seasonality of the occurrence of the tubercles was evident for males and females of both species but was more clearly defined in the males (Tables 1-2 and Fig. 3). Definitive snout tubercles were only present on the males of the two species. The keratinized tips of the definitive tubercles on the heads of both of the redfin minnow species were pointed and curved posteriorly (Fig. 3). In *P. afer* males definitive snout tubercles first appeared in September 1987 and 1988 (Table 1) and there was a close correlation with the seasonal variation in the gonadosomatic indices (Fig. 4). Definitive snout tubercles in *P. asper* males first appeared in October 1987 and in September 1988 (Table 2) and as



Fig. 3. Definitive tubercles on males of *Pseudobarbus afer* (Peters, 1864) (above) and *P. asper* (Boulenger, 1911) (below).



TABLE 2. Summary of the seasonal pattern of tubercle formation and wear in 320 *Pseudobarbus asper* (Boulenger, 1911) males collected over a 22 month period in the Groot River, Gamtoos River system.

Date	n	Size range SL (mm)	Tubercles ¹	Scales ²	Rays ³
July 1987	8	58,6-67,8	B+S	-	-
Aug.	7	58,8-83,4	B+S	-	-
Sept.	14	43,3-64,0	B	+	+
Oct.	15	41,7-64,9	B+D+W	+	+
Nov.	20	40,4-72,3	D	+	+
Dec.	14	45,7-69,9	D	+	+
Jan. 1988	18	45,4-63,1	W	+	+
Feb.	11	42,4-62,0	D+W	+	+
Mar.	6	50,3- 53,7	D	+	+
Apr.	18	34,1-57,6	D+W	+	+
May	10	47,0-58,3	W	-	-
June	16	49,9-65,4	B+S+W	-	-
July	4	48,5-54,5	B+W	-	-
Aug.	10	48,1-70,4	B+S	-	+
Sept.	29	42,8-62,4	B+D	+	+
Oct.	15	42,4-53,9	D+W	+	+
Nov.	20	44,2-63,6	W	+	+
Dec.	16	36,0-64,5	D	+	+
Jan. 1989	19	37,9-61,2	D	+	+
Feb.	13	45,0-66,1	W	+	+
Mar.	12	48,6-71,9	B+D	+	+
Apr.	25	41,7-66,7	B+W	+	+
TOTAL	320				

1. B = bud; D = definitive; S = scars; Sp = spots; W = worn

2. - = absent; + = present

3. - = absent; + = present

with the *P. asper* males there was a close relationship between the seasonal formation of tubercles and the seasonal pattern of the gonadosomatic indices (Fig. 5). The seasonal pattern was also evident in the presence and absence of scale and ray tubercles for both species. The longer potential spawning season of *P. asper* compared to *P. afer* was evident from the presence of definitive tubercles as late as April for *P. asper* males (Figs 4 and 5). In *P. afer* females buds first erupted in September 1987 and 1988 (Table 3). In *P. asper* females buds first appeared in September 1987 and 1988 (Table 4). Tubercles were a dominant feature on the scales and fin rays of the males of both species (Tables 1 and 2) whereas very few females of either species had scale or fin ray tubercles (Tables 3 and 4).

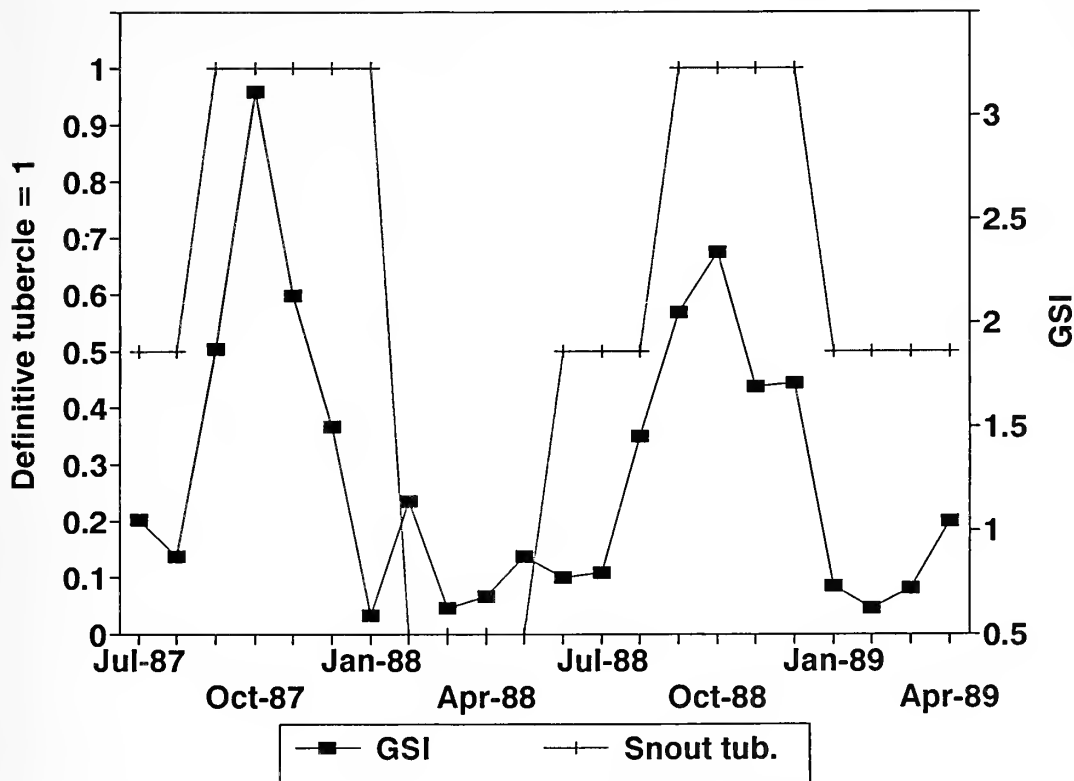


Fig. 4. Comparison of the seasonal occurrence of definitive snout tubercles on male *Pseudobarbus afer* (Peters, 1864) ($n=145$) with the mean monthly gonadosomatic index (GSI) of male *P. afer* for the period July 1987 to April 1989. (Definitive tubercle = 1; bud tubercle = 0,5).

The smallest male *P. afer* with tubercles was 41,2 mm SL, collected in October 1987. Five buds occurred in the posterior dorsal section of this specimen and the pectoral fin rays had tubercles. The smallest male *P. asper* was 39,3 mm SL, collected in January 1989, with three tubercle buds (1 snout and 2 nares).

The smallest female *P. afer* with tubercles (= spots) was 56,5 mm SL collected in December 1988. Two spots were present, one in the nares position and one in posterior dorsal position. The smallest female *P. afer* with buds was a 56,8 mm SL specimen collected in January 1988. There were 6 buds and all were in the posterior dorsal position. In comparison the smallest female *P. asper* with tubercles (= spots) was 49,4 mm SL collected in March 1988. The 4 spots were all in the posterior dorsal position. The smallest female *P. asper* with buds was a 49,5 mm SL specimen collected in October 1987. All 6 buds were in the posterior dorsal position.

A 70,5 mm SL male *P. afer* had the most tubercles of all the males examined for both species with 88 tubercles (14 snout; 7 nares; 12 above orbits; 6 anterior dorsal; 49 posterior dorsal) (Table 5). The biggest tubercles were on the snout and the largest had a volume of $0,89 \text{ mm}^3$ ($b = 1,5 \text{ mm}$; $h = 1,5 \text{ mm}$) (Table 6). In comparison the most tubercles found on male *P. asper* was 53 (6 snout; 6 nares;

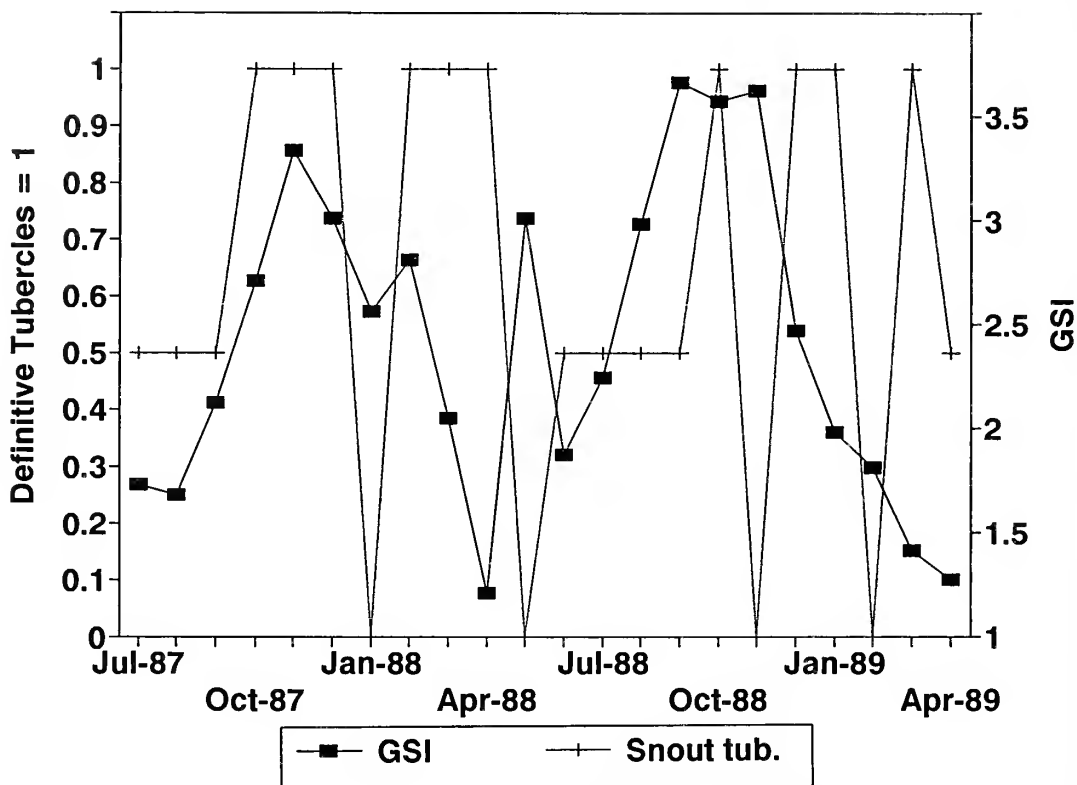


Fig. 5. Comparison of the seasonal occurrence of definitive snout tubercles on male *Pseudobarbus asper* (Boulenger, 1911) ($n=204$) with the mean monthly gonadosomatic index (GSI) of male *P. asper* for the period July 1987 to April 1989. (Definitive tubercle = 1; bud tubercle = 0.5).

3 above orbits; 4 anterior dorsal; 34 posterior dorsal) on a 69.4 mm SL specimen collected during March 1989 (Table 7). There was a highly significant difference ($t=5.50985$, d.f. = 18, $P < 0.001$ of having equal numbers) between number of tubercles on *P. afer* males compared to *P. asper* males. The largest snout tubercle for *P. asper* males had a volume of 0.26 mm^3 (Table 8). There was a highly significant difference ($t = 12.5016$, df = 18, $P < 0.001$ of having an equal volume) between volume sizes of *P. afer* male tubercles compared to the largest *P. asper* tubercles.

There was an increase in the number of tubercles with increasing length for both males (Fig. 6) and females of the two species. The lower correlation coefficient for *P. asper* males and the very low values for the females of both species probably indicated the lack of significance of tubercles for these groups compared to *P. afer* males.

$$\text{Females } P. \text{ afer } y = -12.1037 + 0.233274x \quad (n = 60; r^2 = 0.323)$$

$$P. \text{ asper } y = -33.3291 + 0.694969x \quad (n = 91; r^2 = 0.583)$$

where x = SL (mm); y = number of tubercles

For each separate cluster of tubercles regression analyses were run (Tables 9 and 10). The highest correlation coefficient in *P. afer* males was in the snout tubercles to length and the lowest in the

TABLE 3. Summary of the seasonal pattern of tubercle formation and wear in 118 *Pseudobarbus afer* (Peters, 1864) females collected over a 22 month period in the Wit River, Gamtoos River System.

Date	n	Size range SL (mm)	Tubercles ¹	Scales ²	Rays ³
July 1987	5	52,4-62,5	-	-	-
Aug.	5	57,6-63,0	Sp (few)	-	-
Sept.	5	60,8-70,7	B+Sp	-	-
Oct.	8	67,0-76,1	B+Sp	-	-
Nov.	5	61,0-68,0	W+Sp	-	-
Dec.	5	64,3-68,7	Sp	-	-
Jan. 1988	5	46,8-51,8	-	-	-
Feb.	5	56,8-72,4	B	-	-
Mar.	5	53,4-68,7	B	-	+ (few)
May	5	54,2-61,2	-	-	-
June	5	55,5-60,0	W (few)	-	-
July	5	59,1-72,8	Sp (few)	-	-
Aug.	5	54,9-68,2	-	-	-
Sept.	5	60,6-64,5	B (few)	-	-
Oct.	5	56,4-61,1	B (few)	-	-
Nov.	5	53,2-64,9	-	-	-
Dec.	5	53,4-70,1	Sp	-	-
Jan. 1989	4	52,7-61,1	-	-	-
Feb.	5	54,0-70,5	-	-	-
Mar.	11	58,0 -79,9	B	-	+ (few)
Apr.	5	60,3-65,4	B	-	-
TOTAL	118				

1. B = bud; D = definitive; S = scars; Sp = spots; W = worn; - = absent

2. - = absent; + = present

3. - = absent; + = present

anterior dorsal cluster. Similarly in the tubercle clusters on the head of *P. asper* the snout tubercles had the highest and the anterior dorsal cluster had the lowest correlations with length. In the females of both species there were low correlations for most clusters which had tubercles (Table 10).

The slope of the regression of total tubercle number on standard length of *P. afer* males was significantly different from *P. asper* males ($F = 29,5848$; d.f. = 345; $P < 0,001$; Fig. 6).

In the female sample a 72,4 mm SL *P. afer* had the most tubercles (= spots) for that species. There were 29 spots of which 3 were snout, 4 nares, 4 above orbits, 0 anterior dorsal and 18 posterior dorsal. In the *P. asper* female sample a 72,0 mm SL specimen collected in November 1988 had the most tubercles (including spots). There were 43 spots and buds positioned as follows, 3 (spots) snout, 7 (spots) nares, and 33 (buds) in the posterior dorsal position.

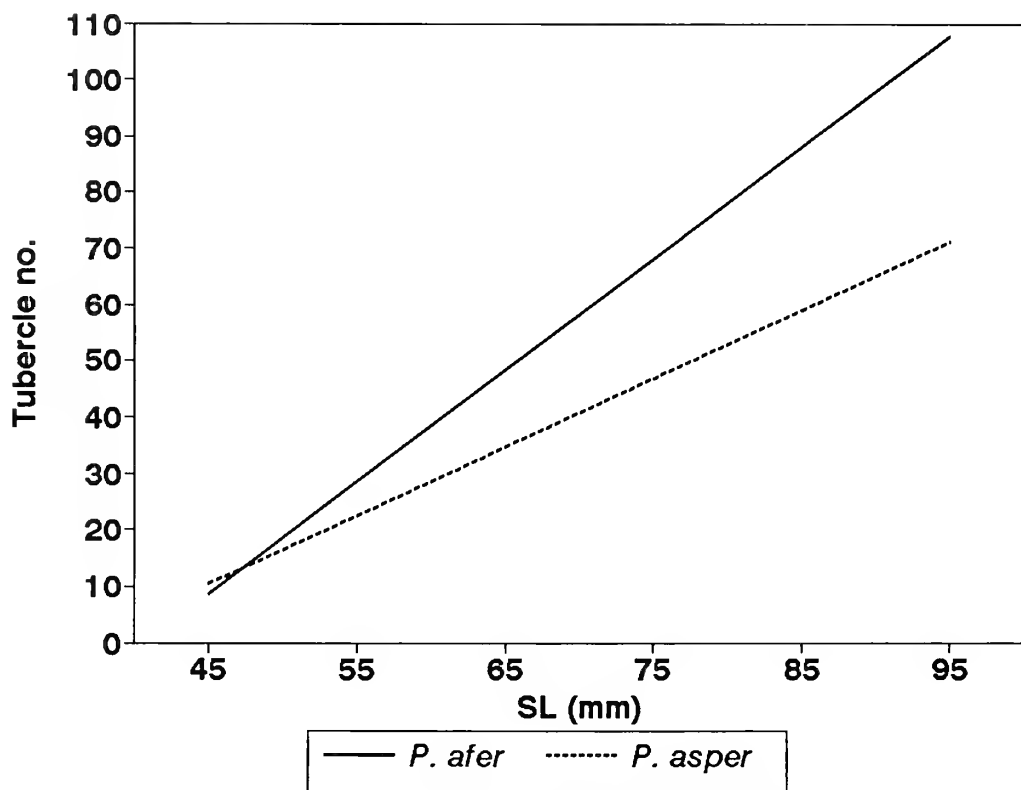


Fig. 6. Relationship between body length and the number of head tubercles in male *Pseudobarbus afer* (Peters, 1864) (n=145) and *P. asper* (Boulenger, 1911) (n=204) collected between September and February 1987/1988 and 1988/1989:
 $P. afer$ $y = -81,2053 + 1,99929x$ (n = 145; $r^2 = 0,878$)
 $P. asper$ $y = -43,659 + 1,20292x$ (n = 204; $r^2 = 0,722$)
 where x = SL (mm); y = number of tubercles

The largest snout tubercle measured was found in the *P. afer* male sample. The volume of the tubercle was $0,89 \text{ mm}^3$ on a 78,2 mm SL specimen (Table 6). In comparison the largest tubercle in the *P. asper* sample was on a 72,3 mm SL male collected in November 1987. The volume of that snout tubercle was $0,26 \text{ mm}^3$ (Table 8). The largest *P. afer* snout tubercle was therefore 3,42 times the volume of the largest *P. asper* tubercle.

In contrast to the males, the female *P. asper* had the most numerous tubercles (= spots or buds) (Tables 11 and 12). The mean number of tubercles for the *P. asper* sample was 30,7 (SD = 6,3) (Table 12) as compared to 12,1 (SD = 7,7) for *P. afer* females (Table 11). Buds or spots were present in the snout, nares and posterior dorsal positions for most specimens. Few spots or buds for both species were observed in the above orbits and interior dorsal positions (Tables 11 and 12). Volumetric calculations were not made for the females as the buds are usually less than $0,002 \text{ mm}^3$. The largest bud measured on a female was on a specimen of *P. asper* ($v = 0,012 \text{ mm}^3$, $b = 0,3$; $h = 0,5$).

Development of tubercles was not always symmetrical. In *P. afer* males, snout tubercles ranged up to 7 on both sides (70,5 mm SL). Of 248 specimens 72 had more tubercles on one side than the other ($X^2 = 145,806$, 1 d.f., $P < 0,0000$). In only two specimens was the difference greater than one.

TABLE 4. Summary of the seasonal pattern of tubercle formation and wear in 157 *Pseudobarbus asper* (Boulenger, 1911) females collected over a 22 month period in the Groot River, Gamtoos River System.

Date	n	Size range SL (mm)	Tubercles ¹	Scales ²	Rays ³
July 1987	3	54,1-56,0	-	-	-
Aug.	3	69,8-76,0	-	-	-
Sept.	11	50,1-69,6	B	-	-
Oct.	4	42,9-57,4	B	-	-
Nov.	6	49,3-63,2	B+Sp	-	-
Dec.	4	50,4-74,3	B+Sp	-	-
Jan. 1988	5	64,7-70,8	Sp	-	-
Feb.	15	50,1-74,1	B+Sp	+ (few)	+ (few)
Mar.	13	45,1-57,8	B+Sp	-	-
Apr.	8	56,7-61,9	B (few)	-	+ (few)
May	4	50,8-60,1	-	-	-
June	5	67,8-72,3	-	-	-
July	4	54,0-63,5	-	-	-
Aug.	4	61,9-74,4	-	-	-
Sept.	5	60,5-79,9	B	-	-
Oct.	5	51,3-70,0	B+Sp	-	-
Nov.	8	65,5-72,2	B+Sp	+ (few)	+ (few)
Dec.	16	54,1-70,7	B+Sp	-	-
Jan. 1989	5	54,5-70,9	B+Sp	-	-
F eb.	9	60,7-76,5	B+Sp	-	-
Mar.	12	62,2-75,2	B+Sp+S	-	-
Apr.	8	59,1-70,9	B+Sp	-	-
TOTAL	157				

1. B = bud; D = definitive; S = scars; Sp = spots; W = worn; - = absent

2. - = absent; + = present

3. - = absent; + = present

Forty-two of the 72 specimens had more tubercles on the left side than on the right ($X^2 = 2,0$, 1 d.f., $P < 0,157299$). In *P. asper* males snout tubercles ranged up to 4 on each side. Of 320 specimens examined, 80 had more tubercles on one side than the other ($X^2 = 200,0$, 1 d.f., $P < 0,0000$). In three specimens the difference was two tubercles. Thirty-seven specimens had more tubercles on the left side than on the right side ($X^2 = 0,225$, 1 d.f., $P < 0,635256$).

The first set of tubercles to show any wear were the snout tubercles followed by the nare clusters for both species. The posterior dorsal tubercles often did not show any sign of wear. No further deductions could be made in the SEM microwear part of this study as no clear patterns of differences in wear were revealed.

TABLE 5. Summary of ten *Pseudobarbus afer* (Peters, 1864) males with the most head tubercles and their position.

Date	SL (mm)	Snout	Nares	Above orbits	Ant. dorsal	Post. dorsal	Total
Nov. 1987	70,5	14	7	12	6	49	88
Dec. 1988	70,1	7	6	10	5	39	67
Oct. 1987	70,8	10	5	8	5	34	62
Feb. 1989	70,5	9	8	7	5	33	62
Oct. 1987	78,2	11	7	7	7	29	61
Feb. 1989	66,2	8	6	8	5	34	61
Sept. 1987	71,5	6	6	6	4	38	60
Sept. 1988	70,5	6	6	7	7	31	57
Jan. 1989	69,6	6	6	10	4	31	57
Dec. 1987	63,4	9	6	5	7	27	54
Means	70,1	8,6	6,3	8	5,5	34,5	62,9
SD	3,8	2,6	0,8	2,1	1,2	6,3	9,5

TABLE 6. Volume of the ten largest snout tubercles found on *Pseudobarbus afer* (Peters, 1864) males collected in the Wit River, Gamtoos River System.

Date	SL (mm)	Base (mm)	Height (mm)	Volume (mm ³)
Oct. 1987	78,2	1,5	1,5	0,89
Nov. 1987	58,0	1,6	1,0	0,67
Nov. 1987	70,5	1,3	1,5	0,67
Sept. 1987	63,2	1,25	1,05	0,43
Dec. 1987	63,4	1,1	1,1	0,35
Dec. 1987	58,1	1,2	0,9	0,34
Dec. 1987	49,5	1,2	0,85	0,32
Oct. 1987	60,9	1,2	0,7	0,26
Oct. 1987	57,3	1,2	0,6	0,23
Nov. 1988	59,7	1,1	0,6	0,19
Means	61,9	1,27	0,98	0,44
SD	7,9	0,16	0,33	0,23

TABLE 7. Summary of ten *Pseudobarbus asper* (Boulenger, 1911) males with the most head tubercles and their position.

Date	SL (mm)	Snout	Nares	Above orbits	Ant. dorsal	Post. dorsal	Total
Mar. 1989	69,4	6	6	3	4	34	53
Dec. 1987	69,9	6	6	3	6	30	51
Nov. 1987	72,3	8	6	2	2	31	49
Dec. 1987	64,6	6	6	4	4	24	44
Jan. 1988	63,1	6	6	1	1	29	43
Aug. 1988	70,4	8	6	3	5	20	42
Sep. 1987	62,4	6	6	4	1	24	41
Apr. 1989	66,6	6	6	5	2	21	40
Dec. 1988	59,7	6	6	1	8	18	39
Feb. 1989	65,9	8	6	3	0	22	39
Means	66,4	6,6	6	2,9	3,3	25,3	44,1
SD	4,0	1,0	0,0	1,3	2,5	5,4	5,1

TABLE 8. Volume of the ten largest snout tubercles found on *Pseudobarbus asper* (Boulenger, 1911) males collected in the Groot River, Gamtoos River System.

Date	SL (mm)	Base (mm)	Height (mm)	Volume (mm ³)
Nov. 1987	72,3	1,2	0,7	0,26
Dec. 1988	64,5	1,2	0,7	0,26
Feb. 1989	66,1	1,0	0,9	0,24
Jan. 1989	55,5	1,0	0,8	0,21
Sep. 1988	58,8	1,0	0,7	0,18
Dec. 1988	60,4	1,0	0,7	0,18
Dec. 1988	56,4	0,9	0,8	0,17
Feb. 1988	56,0	1,0	0,5	0,13
Dec. 1988	62,3	0,8	0,7	0,12
Dec. 1988	59,7	0,8	0,7	0,12
Means	61,2	1,0	0,72	0,19
SD	5,3	0,14	0,1	0,05

TABLE 9. Linear regression analyses of the number of tubercles in the different clusters (see text) on the heads to length of male *Pseudobarbus afer* (Peters, 1864) and *P. asper* (Boulenger, 1911).

Tubercle cluster	n	a	b	r
<i>P. afer</i> ♂ ♂				
Total	143	-80,332	1,980	0,878
Snout	143	-12,664	0,307	0,883
Nare	143	-7,951	0,233	0,748
Orbit	143	-12,968	0,296	0,867
Ant. dorsal	143	-7,784	0,181	0,739
Post. dorsal	143	-38,965	0,964	0,773
<i>P. asper</i> ♂ ♂				
Total	202	-44,017	1,210	0,722
Snout	202	-6,366	0,206	0,685
Nare	202	-6,127	0,195	0,601
Orbit	202	-3,052	0,067	0,504
Ant. dorsal	202	-3,257	0,075	0,407
Post. dorsal	202	-25,216	0,666	0,643

TABLE 10. Linear regression analyses of the number of tubercles in the different clusters (see text) on the heads to length of female *Pseudobarbus afer* (Peters, 1864) and *P. asper* (Boulenger, 1911).

Tubercle cluster	n	a	b	r
<i>P. afer</i> ♀ ♀				
Total	60	-12,104	0,233	0,323
Snout	60	-2,195	0,040	0,404
Nare	60	-6,463	0,117	0,525
Orbit	60	-33,329	0,695	0,583
<i>P. asper</i> ♀ ♀				
Total	91	-33,329	0,695	0,583
Snout	91	-5,558	0,113	0,484
Nare	91	-4,587	0,093	0,431
Post. dorsal	91	-22,671	0,479	0,523

TABLE 11. Summary of ten *Pseudobarbus afer* (Peters, 1864) females from Wit River, Gamtoos River system, with the most head tubercles and their position.

Date	SL (mm)	Snout	Nares	Above orbits	Ant. dorsal	Post. dorsal	Total
Feb. 1988	72,4	3	4	4	0	18	29
Dec. 1987	68,4	2	8	2	2	6	20
Feb. 1988	57,0	0	0	0	0	16	16
Mar. 1989	70,7	2	5	0	1	6	14
Feb. 1988	58,1	0	0	0	0	10	10
Mar. 1989	63,9	2	4	0	0	1	7
Sep. 1987	61,7	2	3	0	0	2	7
Feb. 1988	56,8	0	0	0	0	6	6
Sep. 1987	70,3	0	4	1	0	1	6
Oct. 1987	72,6	2	4	0	0	0	6
Means	65,2	1,3	3,2	0,7	0,3	6,6	12,1
SD	6,4	1,2	2,6	1,3	0,7	6,3	7,7

TABLE 12. Summary of ten *Pseudobarbus asper* (Boulenger, 1911) females from the Groot River, Gamtoos River system, with the most head tubercles and their position.

Date	SL (mm)	Snout	Nares	Above orbits	Ant. dorsal	Post. dorsal	Total
Nov. 1988	72,0	3	7	0	0	33	43
Mar. 1989	68,5	6	6	0	0	29	41
Feb. 1988	74,1	2	4	0	0	27	33
Nov. 1988	72,2	4	3	4	0	18	29
Feb. 1989	76,5	6	4	0	0	18	28
Feb. 1988	66,4	2	4	0	0	21	27
Feb. 1988	65,2	2	3	0	0	22	27
Nov. 1988	70,1	6	4	0	0	17	27
Mar. 1989	75,2	4	4	0	0	19	27
Sep. 1987	68,0	2	4	0	0	19	25
Means	70,8	3,7	4,3	0,4	0	22,3	30,7
SD	3,8	1,8	1,3	1,3	0	5,5	6,3

DISCUSSION

Nuptial or breeding tubercles can develop on the head, fins and bodies of fish. They are present in regions which come into contact with another male or female fish. The seasonal occurrence and disappearance of tubercles follows the reproductive cycle and is probably under seasonal hormonal control. There are several possible functions for these structures on males: fighting other males or invaders, the white colour of the tubercles might denote spawning readiness; used to maintain body contact during spawning; stimulation of females during spawning; protection of the body and fins from damage during nest construction; tubercles on the ventral surface of females may protect the anus and urogenital papillae against mechanical damage during egg laying; to hold the substrate in swift waters during the spawning act; and to take care of the eggs, nest and young (Hubbs and Cooper, 1936; Raney, 1940; Fabricius and Gustafson, 1955; Branson, 1961, 1962; Koehn, 1965; Braasch and Smith, 1967; Wiley and Collette, 1970; Collette, 1977; Kratt and Smith, 1978; Cambray and Stuart, 1985). The tubercles of the males may reflect a pearly hue which may attract females. Since there are different patterns for different species, tubercles may aid in species and sex recognition. Collette (1977) suggested that breeding tubercles originally evolved to enable breeding individuals to maintain close contact during spawning. In fishes which breed in fast-flowing waters close contact would ensure fertilization of the eggs. The possible functions of the nuptial tubercles on the rays, scales and head for male *P. afer* and *P. asper* are summarised in Table 13.

TABLE 13. Possible functions of the breeding tubercles of male *Pseudobarbus afer* (Peters, 1864) and *P. asper* (Boulenger, 1911).

Function	<i>P. afer</i> (clear water)	<i>P. asper</i> (turbid)
Maintain contact during spawning (tactile; scale and ray tubercles)	Possible	Possible
Holding to the substrate during spawning in swift flowing waters (scale, ray and head tubercles)	Possible	Possible
Stimulation of females (head tubercles)	Possible	Possible
Excavating a nest (head tubercles)	Unlikely	Unlikely
Defense of nests (head tubercles)	Unlikely	Unlikely
Fighting other males (head tubercles)	Possible	Possible
Visual threat (head tubercles)	Possible	Unlikely
Sex recognition (head tubercles)	Possible	Unlikely
Species recognition (head tubercles)	Possible	Unlikely

Tubercles were better developed on males of both *P. afer* and *P. asper* than females. The largest tubercles were found on *P. afer* males and were up to 3,42 times the volume of the largest tubercles on male *P. asper* (Tables 6 and 8). As in the present study Kratt and Smith (1978) and Witkowski (1982 in Witkowski and Ragowska, 1991) found that tubercles were better developed on those fish

which have spawned several times than on first time spawners. Secondary sexual characteristics, such as epidermal tubercles and breeding coloration, all require resources which must be diverted away from growth and survival requirements (Miller, 1979; Wootton, 1985). The formation of and the subsequent behaviour of fish with tubercles would probably be energetically costly which would reduce growth. If females developed large tubercles with associated behaviour then this allocation of energy to secondary sexual characteristics could possibly reduce the future production of offspring. This would favour the development of these characters on males only (Wootton, 1990). Large females of *P. afer* and *P. asper* have head tubercles which are never definitive and their presence on reproductively active females was difficult to explain. Why should the larger females of *P. afer* and *P. asper* have invested any energy into producing tubercles? The females with tubercles had high gonadosomatic indexes and therefore were not senescent and there was no evidence of hermaphroditism. When tubercles occurred on the head they followed the pattern exhibited on the males (Fig. 2). That very few females were found to have tubercles on their rays indicated that they did not use them for maintaining position during mating and the occurrence of rudimentary head tubercles on the large females may merely indicate a hormonal change as the fish grew older. *Pseudobarbus asper* females were found to have more head tubercles than *P. afer* females. There was no obvious adaptive significance to the bearer and, if anything, the allocation of resources to produce weakly developed tubercles would decrease female fitness.

The nuptial tubercles on the pectoral fins of some cyprinids may be used in a 'pectoral fin lock' in which the male clasps the female (Branson, 1962). The tubercles on the fin can be recurved which would facilitate clasping. Boulenger (1911) noted sexual dimorphism in the pectoral fins of *P. asper* with males having longer pectoral fins than females. Sexual dimorphism of the fins and length of pectorals relative to the base of the pelvis was later found to be evident in most of the flexible-rayed redfins (Barnard, 1943). Male *P. afer* and *P. asper* have broader and more rounded pectoral fins than females (Skelton, 1988). The males may use the larger, longer and broader pectoral fins with more tubercles for clasping the female during spawning (pectoral fin lock). Cambray and Meyer (1988), Cambray (1991) and Cambray (1992) have noted that *P. afer*, *P. asper* and *P. quathlambae* bred in mid-channel riffles after an increase in flow. Clasping of the pectoral fins, aided by increased size and tubercles on the rays of these fins, would be advantageous to ensure fertilization of the eggs especially in the fast-flowing water of the spawning habitat. The tubercles present on the scales would also help to maintain a spawning embrace. The large tubercles on the head must have a different purpose and would not be used for clasping. It is therefore in the head tubercles that one may expect differences in size and/or density between species inhabiting clear or turbid waters.

The head tubercles may be for interactions between males to acquire mates (intrasexual selection) or for interactions between the sexes to choose mates (intersexual selection). The dorsal tubercles of the head and trunk in many species are usually fairly well developed, possibly because they are used for fighting invaders or other males, and attracting and nudging females during spawning. Tubercle rows over the orbits might be a protective mechanism during agonistic behaviour of *P. afer* or *P. asper* males, as was suggested for some *Nocomis* species (Lachner and Jenkins, 1971). Because of the highly turbid waters in which *P. asper* lives, it would be unlikely that this species used head tubercles for visual threat, sex recognition or species recognition (Table 13). But as *P. afer* inhabits clear waters they could be used for the above functions (Table 13). If the tubercles were used to nudge the female during spawning then that would not help to explain the smaller tubercles of *P. asper* males. There was no obvious evidence for how the tubercles were used in the flexible-rayed redfins and the scanning electron microscopy microwear study did not elucidate the probable cause(s) of the observed wear of the head and ray tubercles during the reproductive season.

One of the most notable characters of sexually mature male *P. burchelli* were the large conical head tubercles (Cambray and Stuart, 1985) which are more highly developed than in most other *Pseudobarbus* and small *Barbus* species (Skelton, 1980). Cambray and Stuart (1985) have noted the seasonal occurrence, wear, number and size of the breeding tubercles of both male and female *P. burchelli*. As in *P. afer* and *P. asper* the head tubercles of *P. burchelli* were more developed on males as compared to females. Larger males were found to have larger tubercles. The large conical tubercles on the heads of the males (> 80 mm FL) began to erupt in May. The tubercles were found to erupt through the worn tubercle bases of the previous season. Some tubercles were well formed by August and the first signs of wear occurred in November which coincided with the spawning season. In *P. burchelli* the wearing and/or sloughing off of the tubercles continued until April when only the bases of the tubercles were visible. Cambray and Stuart (1985) suggested that this seasonal cycle of tubercle formation and wear added support to the hypothesis that the tubercles were associated with reproduction in redbfin minnows (Skelton, 1980). It was proposed by Cambray and Stuart (1985) that the wearing as the season progressed suggested that the tubercles are used when defending a territory. The keratin caps get worn off as the breeding season progresses.

The lifetime reproductive success of individuals may be influenced by the individual variation in tubercle number and/or size. In male *P. afer* the head tubercles were both volumetrically larger and more numerous than those of *P. asper*. That would suggest that in the clear water habitat of *P. afer* size and number of tubercles were important for reproductive success and may have influenced mate choice. The presence of tubercles may signal information about the genetic quality of the bearer, or it may only be that the presence of large tubercles and bright red coloration makes the bearer more likely to be chosen by a potential mate. The ultimate factors which have lead to the evolution of the secondary sexual characters, such as tubercles, are still a subject of debate (Wootton, 1990). In New World cyprinids, sexual differences are usually more pronounced in those species that are highly territorial, have some form of parental care, or carry out their life cycles in high-gradient and clear rivers (Mayden, 1991). There is no known parental care in *Pseudobarbus* species but most of the species, such as *P. afer* and *P. burchelli*, inhabit clear water systems.

Quantitative differences in secondary sexual characters of a species may play a role in mate discrimination by reinforcing speciation once populations that had diverged in allopatry came back into contact (Dobzhansky, 1940). The noted differences in secondary sexual characters of *P. afer* and *P. asper* males may reinforce speciation in the Groot River as there is no physical barrier separating these two species (Cambray, 1992).

Pseudobarbus afer, *P. asper* and *P. quathlambae* (Cambray and Meyer, 1988; Cambray, 1991; Cambray, 1992) all spawned after an increase in river flow and their spawning habitat was mid-channel amongst boulders. Ozarkian minnows which were very active spawners or which spawned in rapidly flowing waters were found to have more extensively developed, scattered tubercles than sedentary species which had tubercles in lines (Branson, 1962). Cyprinids with unspecialized breeding habits usually have small tubercles distributed over the head in no particular pattern (Lachner and Jenkins, 1971). This may indicate that in the *Pseudobarbus* species with large tubercles, such as *P. afer* and *P. burchelli*, there may be more specialized breeding habits compared to species such as *P. asper* and especially *P. phlegethon* which have smaller or vestigial tubercles. This difference requires further investigation.

It is suggested that in *P. afer* and *P. asper* males large head tubercles are used for display prior to breeding, whereas during breeding the tubercles on the scales and fin rays maintain contact with females, as do the larger pectoral fins of the males, in the riffle spawning habitat. The occurrence of fewer and smaller tubercles on *P. asper* males may be because in turbid waters visual characters have

less of a selective advantage than in a clear mountain stream (Table 13). That the head tubercles are still relatively large in *P. asper* may be a phylogenetic constraint within the sister species pair.

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A new subspecies of the freshwater halacarid mite *Lobohalacarus weberi* (Romijn and Viets) (Halacaridae, Acari) from a Southern Atlantic Ocean island

by

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ABSTRACT

Lobohalacarus weberi tristanensis **subsp. nov.**, found on Inaccessible, Tristan da Cunha Islands, is described and compared with populations of *L. weberi weberi* (Romijn and Viets) from Europe. Representatives of the *Lobohalacarus weberi* complex primarily inhabit subterranean waters. A short survey of species and subspecies of the *L. weberi* complex is given and means of dispersal to Inaccessible Island are discussed.

INTRODUCTION

Although comprising mostly marine species, the superfamily Halacaroidae includes several freshwater species. At present, about 700 marine and 50 limnic species are described. The freshwater halacarid species differ from marine species in having external genital acetabula. The freshwater species can be assigned to several halacarid subfamilies.

AREA OF INVESTIGATION, MATERIAL AND ABBREVIATIONS

The Tristan da Cunha island group lies about midway between South Africa and South America, in a belt with prevailing westerly winds and easterly water currents (Baker *et al.*, 1964). The islands, of volcanic origin, are located east of the mid-Atlantic Ridge. Inaccessible, the most westerly island, has an area of about 10 km and reaches a height of 550 m (Baker, 1973). The island is resting on an older eroded volcanic cone, about 18 million years old (Baker *et al.*, 1964; Chevallier *et al.*, 1992).

The halacarid specimens were collected on the west side of Inaccessible Island, from a small, narrow freshwater stream bordered by *Spartina arundinacea*. The sampling site is less than 1 km from the underground source of the stream; the water is clear, pH 7.0 (Barber-James, in prep).

Abbreviations used in the descriptions are: AD, anterior dorsal plate; AE, anterior epimeral plate; br, bristle; GA, genitoanal plate; GO, genital opening; OC, ocular plate(s); P, palp, P-2, 2nd palpal segment; pas, parambulacral setae; PD, posterior dorsal plate; PE, posterior epimeral plate; sp, spine. Legs are numbered I to IV, leg segments 1 to 6 (I-1, I-2, I-3, I-4, I-5, I-6 = trochanter, basifemur, telofemur, genu, tibia and tarsus on leg I).

The type material is deposited in the Albany Museum, Grahamstown, South Africa.

TAXONOMY

***Lobohalacarus weberi tristanensis* subsp. nov.**

MATERIAL

One holotype female, Albany Museum, Grahamstown, TDC II H; Inaccessible Island, from

narrow freshwater stream; collected by H.M. Barber-James, 23 October 1989.

Three paratype females, one larva, Albany Museum, Grahamstown, TDC I G; type locality. Two females, author's halacarid collection, type locality.

DESCRIPTION

Holotype female. Idiosoma 310 μm long. Integument of dorsal plates foveate and delicately punctate. Anterior rounded idiosoma formed by dorsal portion of AE which is fused in midline. Anterior AD contiguous but not broadly joined with that area. AD 92 μm long; with an area like an inverted Y slightly raised (Fig. 1). AD with 18-20 foveae in width and 17 foveae in length. OC elongate, 75 μm long; no cornea present. PD 184 μm long, with two slightly raised longitudinal costae; transversely about 20-22 foveae wide, longitudinally with 27-29 foveae. Dorsal idiosomatic setae small; one pair of setae inserted anterior to the AD, one pair on the AD on a level with insertion of leg I, one pair each in anterolateral edge and near medial edge of OC. PD with three pairs of setae, one of them on a level with insertion of leg III, one on that of leg IV, and one pair of setae in posterior PD.

Ventral shield (fused anterior epimeral plate, posterior epimeral plate and genitoanal plate) delicately foveate and punctate. Area corresponding to AE with three pairs of long ventral setae and one pair of epimeral pores (Fig. 2); area of PE with one dorsal, one long lateral and one ventral seta. GO 70 μm long; genital sclerites with two pairs of acetabula. These acetabula in size and morphology similar to epimeral pores. Area of GA with two and four perigenital setae (asymmetrically). Ovipositor short, in rest hardly extending beyond the GO.

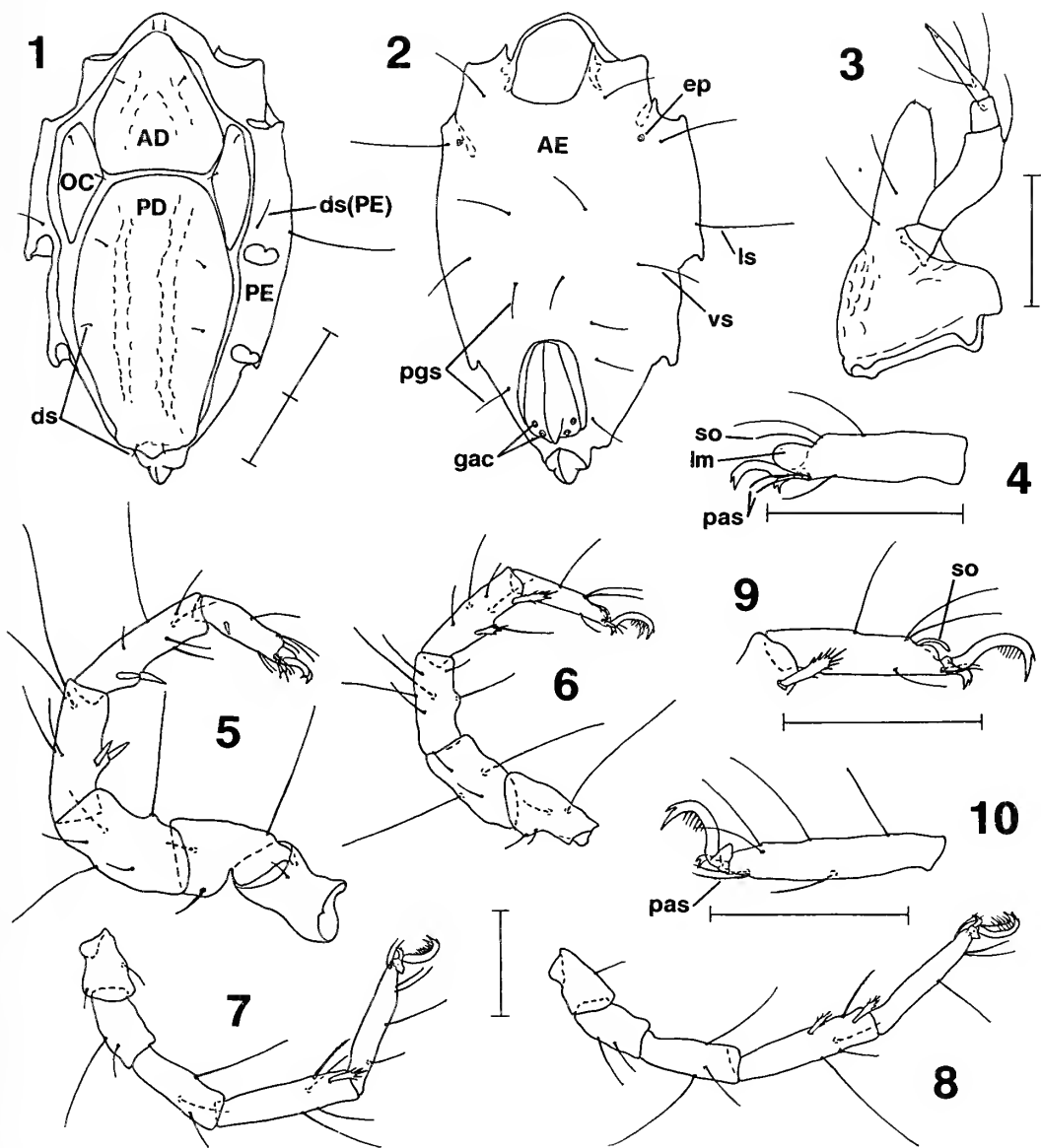
Gnathosoma 108 μm long, with rostrum and gnathosoma base similar in length. Both pairs of maxillary setae inserted near the rostral base. Palps 4-segmented; P-2 with one long dorsal seta; P-3 with medial spine; P-4 with three basal setae (Fig. 3).

Leg I stouter than posterior legs. All legs with basifemora and telofemora subequal in length. Genu I slightly longer than telofemur I (Fig. 5), II-4 slightly shorter than II-3 (Fig. 6), and genua on legs III and IV longer than telofemora, respectively (Figs 7 and 8). All tibiae longer than genua. Number of setae, from trochanter to tarsus (pas and solenidion included): leg I, 1, 3, 5, 6, 8, 11; leg II, 1, 4, 4, 6, 7, 7; leg III, 1, 2, 2, 3, 5, 6; leg IV, 0, 1, 2, 3, 6, 5. Genu I ventrally with two short spines, I-5 with basal pair of short spines and distal pair of bristles. Tibiae II and IV with one slender ventral bristle and two short and pectinate bristles; tibia III with one seta and one pectinate bristle. Tarsus I with one ventromedial spine, two short ventral setae and three long dorsal setae, tip of tarsus with seta-like dorsolateral solenidion, conspicuously large lateral membrane (Fig. 4) and doubled lateral and medial pas. Solenidion on tarsus II hollow, dorsomedial in position (Fig. 9). Number of dorsal/ventral setae on tarsi II to IV: 3/1, 3-4/0-1 (asymmetrically), 3/0; posterior tarsi with a pair of single pas.

Pair of claws on tarsus I smaller than on posterior tarsi; claws with accessory process but without long pecten. Claws on tarsi II to IV with pectens bearing long tines.

Male. Unknown.

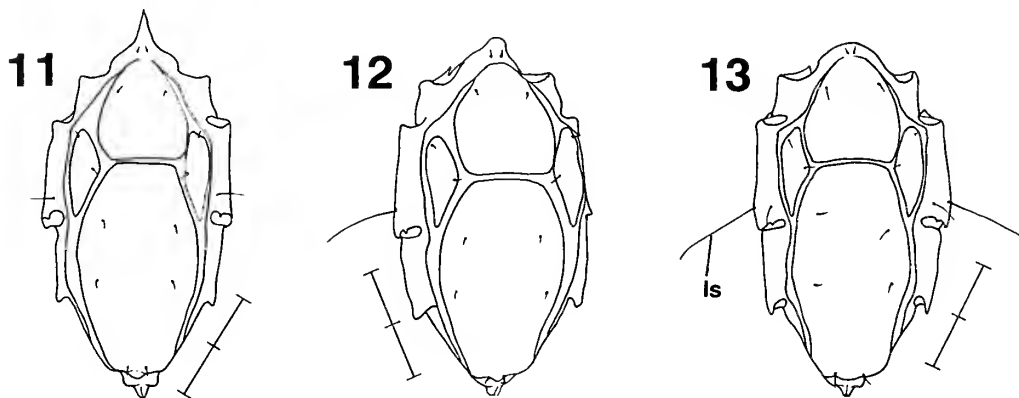
Juveniles. Deutonymph and protonymph unknown. Larva 185 μm long. Dorsal plates foveate. Anterior margin of idiosoma truncate. Number of dorsal setae same as in adults but first pair of setae in anterior margin of idiosoma, and third pair of setae inserted within the striated integument anterior to the OC. PD much smaller than in the female. Ventral plates separate. Genital plate lacking. Larva with three pairs of 5-segmented legs. Genu and tibia I each with a pair of spines but no ventral bristles.



Figs 1-10. *Loboahalacarus weberi tristanensis* **subsp. nov.**, female; 1. idiosoma, dorsal; 2. idiosoma, ventral; 3. gnathosoma, lateral; 4. tarsus I, lateral (medial setae and claw omitted); 5. leg I, medial; 6. basifemur to tarsus II, medial; 7. basifemur to tarsus III, medial; 8. basifemur to tarsus IV, medial; 9. posterior tibia and tarsus II, medial (lateral claw omitted); 10. tarsus III, medial (lateral claw omitted). 1-9, holotype female; 10, paratype female. (AD, anterior dorsal plate; AE, anterior epimeral plate; ds, dorsal setae; ds(PE), dorsal seta on PE; ep, epimeral pore; gac, genital acetabula; lm, lateral membrane; ls, lateral seta; OC, ocular plate; pas, parambulacral setae; pgs, perigenital setae; PD, posterior dorsal plate; PE, posterior epimeral plate; so, solenidion; vs, ventral seta)

VARIABILITY

Length of females 310-341 μm (with frontal spine included) or 301-314 μm (frontal spine excluded). The females proved to be highly variable in external characters. Three of the specimens have an elongate and spine-like anteromedian idiosomatic extension (Fig. 11), one specimen has a short and rounded frontal hood (Fig. 12), and in two of the females, the anterior idiosoma is rounded (Fig. 13). The number of perigenital setae varies from two to four setae and the number of genital acetabula from one to two on either side. In the majority of species, the PE have one dorsal, one lateral and one ventral seta, but the dorsal seta may be lacking (Fig. 12). Bilateral asymmetry in the leg chaetotaxy is fairly common, e.g., in four specimens both genua I have a pair of ventral spines; in one specimen both genua I bear a long and slender ventrolateral seta and a short ventromedial spine; another specimen has a pair of spines on the left genu but a ventromedial spine and a ventrolateral seta on the right genu. Tibiae II each bear one seta-like ventral bristle, and either one (1 specimen, unilaterally) or two wide and bipectinate bristles; tibiae III have one ventral seta-like bristle plus one (5 specimens) or two (1 specimen) wide and pectinate bristles; tibiae IV all have ventrally one seta-like and two pectinate bristles. Tarsi III generally bear four dorsal setae (Fig. 10), though, in the holotype, one tarsus has no more than three dorsal setae. One specimen has a ventral seta on both tarsi III, the other five specimens demonstrate asymmetry with either one or no ventral setae.



Figs 11-13. *Lobohalacarus weberi tristanensis* **subsp. nov.**, female, dorsal variants of idiosoma; 11. with frontal spine; 12. with frontal hood (idiosoma with left lateral seta on PE); 13. anteriorly rounded (idiosoma with lateral setae on PE). (ls, lateral seta) Scale bars = 50 μm .

REMARKS

The specimens from Inaccessible Island undoubtedly belong to the *Lobohalacarus weberi* complex, a group of closely allied species and subspecies with records from Europe, Asia, Africa, Australia, South and North America.

The specimens from Inaccessible Island are given the rank of a subspecies, viz., *Lobohalacarus weberi tristanensis*. The population demonstrates a much higher tendency to variability than found in the nominate form *L. weberi weberi* (Romijn and Viets) in Europe. Most remarkable is the anterior idiosoma, arch-like, with small rounded tip or with long spine-like projection. In contrast, specimens from Europe, as well as species and subspecies from other geographical regions, always have a spine-

like process. Telfemora III and tarsi IV have two and three dorsal but no ventral setae whereas in the European *L. w. weberi* these segments bear ventral setae.

GEOGRAPHICAL AND BIOLOGICAL SURVEY

The genus *Lobohalacarus* is world-wide in distribution. It includes species and subspecies which are closely allied and belong to a single natural complex, the *Lobohalacarus weberi* group. *L. weberi* was described on the basis of a specimen collected in The Netherlands (Romijn and Viets, 1924). The species proved to be widely distributed in Europe, Africa, North America and the Hawaiian Islands (Viets, 1950; Imamura, 1981; and unpublished records), generally inhabiting hypogean (hyporheic) and epigean waters fed by groundwater. *L. bucharensis* Jankovskaja, known from juveniles only, was found in groundwater in Middle Asia (Jankovskaja, 1967, 1972). *L. bumrong* Harvey is a hyporheic Australian species (Harvey, 1988), and *L. hummelincki* Viets was taken on the bank of a river in Venezuela (Viets, 1940). *L. processifer* (Walter) is known from a juvenile from a lake in the Andes, at 5000 m (Walter, 1919), and *L. weberi gotoensis* Imamura is a stygobiontic species from lava caves, Japan (Imamura, 1970). *L. weberi tristanensis* was collected from a small stream, together with the oribatid mite *Trimalaconothrus* sp. (Barber-James, in prep.).

Lobohalacarus primarily inhabits subterranean waters and areas where hypogean waters meet the surface. *Lobohalacarus w. weberi* prefers darkness (unpublished experiments). The specimens generally live in constantly waterlogged substrates, but they are known to survive in moist sand, within the water-film, for more than a month (Teschner, 1961). *L. w. weberi* can withstand marine conditions for a couple of hours, and brackish water with a salinity of 20 or 10 ppt for about one or two to three weeks respectively (unpublished preliminary experiments with a population from northern Germany, from a pond with *Sphagnum* fed by groundwater).

Lobohalacarus weberi is thought to be primarily parthenogenetic (Bartsch, 1981). The fecundity is low, probably a single generation per year and no more than 10 eggs per female (Teschner, 1963). The eggs are carefully deposited in the substrate, e.g., sand (Teschner, 1963). They are not conspicuously thick-walled, but still they may be more tolerant to both desiccation and higher salinities than are adults.

MORPHOLOGICAL VARIANTS AND CHARACTERISTICS IN *LOBOHALACARUS*

Representatives of the genus *Lobohalacarus* are characterized by : Idiosoma with seven pairs of dorsal setae (adanal setae included, dorsal seta on PE excluded); genital sclerites with acetabula; palps four-segmented; third palpal segment with median spine; slender fourth palpal segment with three setae in the basal whorl; genu I nearly as long as telfemur or tibia I; tarsus I with three dorsal seta, dorsolateral solenidion, one ventromedial spinelet or seta, pair of ventral setae, and pair of apical parambulacral setae; lateral membrane of claw fossa enlarged.

Lobohalacarus differs from the majority of halacarids in having seven pairs of dorsal idiosomatic setae but no gland pores. All closely related marine and freshwater genera, and the majority of halacarid genera in general, have six pairs of dorsal setae and one to five pairs of gland pores. Five pairs are thought to be the original number of pores. The first pair of pores are almost always present, while the other pores may be greatly reduced, absent or replaced by setae. Substitution by setae is found in the majority of species of the genus *Rhombognathides* and *Metarhombognathus* (Bartsch, 1992), and in at least one species of *Lohmannella* (Bartsch, 1993). In species of the *L. weberi* complex, the anterior pair of setae is believed to correspond with the first pair of dorsal setae regularly present in

halacarid mites, whereas the pair of setae in the lateral margin of AD may originate from gland pores.

The author's halacarid collection includes more than a hundred specimens of *Lobohalacarus weberi*, from Europe (northern Baltic, northern Germany, Spain), northeastern America (Rhode Island), and the Hawaiian Archipelago; the specimens were collected from various substrates such as groundwater wells, ponds and small streams with mosses and pH as low as 4.5-5.0, and fine sand, more or less rich on organic material, pH-values of 6.0-7.8, and also slightly influenced by brackish water.

Variability was studied on populations from Europe and the United States, viz., 20 specimens each from two sites in Germany, and a small number of specimens from northern Baltic, Spain, Rhode Island (Table 1) and Hawaiian Islands.

Characters known to vary in *Lobohalacarus* are:

Frontal spine. The nominate species *L. w. weberi* always has a frontal spine.

Genital acetabula. The majority of subterranean living species have two pairs of genital acetabula whereas specimens from epigeal waters, such as lakes, ditches, and habitats influenced by slightly brackish waters, have three pairs of genital acetabula. But, generally, within a population (sample) both variants are present, asymmetry is fairly common. In populations from northern Germany, 77-97 % of the specimens had genital sclerites with two acetabula. Specimens with a small, primordial acetabulum beside the one or two well developed genital acetabula are present, too.

Number of perigenital setae. The most common variant in European populations are five pgs on either side. About 15-25 % of the specimens in a given population, from both Europe and America, have four pairs of setae. The combinations 2/4 (two setae on one side, four setae on the other side), as well as 6/5 have been found in a population from Germany.

Geni I. The majority of specimens have the combination sp/br, that is ventromedially a spine and ventrolaterally a bristle. In the two populations from Northern Germany, 2-6 % had spines both ventromedially and ventrolaterally, asymmetrically or on both legs. Exceptionally, the spine or seta is lacking.

Tibia II. Most specimens have one ventral seta and two wide, pectinate ventromedial bristles. A single bipectinate bristle (aside from the ventral seta) is found in 0-20 % of the specimens in a given population. One specimen from the Northern Baltic had two pectinate bristles and two smooth and slender setae.

Tibia III. Most abundant are two ventral bristles, one short and bipectinate, the other longer, seta-like and very faintly plumose. Though, in populations from northern Germany and northeast America, 30-40 % of the specimens had three ventral bristles, with two of them being wide and coarsely pectinate.

Tibia IV. They generally have three ventral bristles, one of them is seta-like and slender, two are wide and pectinate. Exceptions, viz., tibiae with two ventral bristles, one wide and pectinate, the other slender, seta-like and delicately plumose, are very rare.

Telofemur III. The specimens from the northern Baltic and northern Germany all have the chaetotaxal combination 2/1 (two dorsal and one ventral setae), whereas specimens from Spain and from eastern America either had 2/1 or 2/0 setae.

Telofemur IV. Both combinations 2/1 and 2/0 are commonly represented.

Tarsus III. Four dorsal and one ventral seta is the most common variant, other combinations are found, though only unilaterally.

Tarsus IV. Generally, 3/1 (three dorsal and one ventral) setae are present. The combination 3/0 has been found, unilaterally, in two specimens from northeastern America. Specimens with two ventral setae, instead of one, have been seen in European and northern American populations.

TABLE 1. *Lobohalacarus weberi*, variants of characters and, in brackets, percentage of variants in populations from: Northern Germany, population A (groundwater well), population B (bog with *Sphagnum*); Northern Baltic (muddy sand, brackish water); Rhode Island (riverines with *Sphagnum*); Inaccessible Island (river with *Spartina*).
(br = bristle; d/v = dorsal/ventral; sp = spine)

Populations from	Northern Germany A B		Northern Baltic	Rhode Island	Inaccessible Island
Character					
Anterior AD	spine (100)	spine (100)	spine (100)	spine (100)	spine (50) hood (17) rounded (33)
Number of genital acetabula	2 (97) 1 1/2 (3)	3 (19) 2 1/2 (3) 2 (77)	3 (71) 2 (29)	3 (5) 2 (95)	2 (83) 1 (17)
Number of perigenital setae	5 (68) 4 (26) 3 (6)	6 (4) 5 (77) 4 (15) 2 (4)	5 (94) 4 (6)	5 (74) 4 (26)	4 (42) 3 (42) 2 (16)
I-4, combination of sp and br	sp/br(96) sp/sp (2) 0/br (2)	sp/br (94) sp/sp (6)	sp/br (100)	sp/br (100)	sp/br (25) sp/sp (75)
II-5, number of pectinate bristles	2 (100)	2 (87) 1 (13)	2 (100)	2 (80) 1 (20)	2 (92) 1 (8)
II-5, number of pectinate bristles	1 (100)	1 (58) 2 (42)	2 (100)	1 (67) 2 (33)	1 (83) 2 (17)
IV-5, number of pectinate bristles	2 (92) 1 (8)	2 (100)	2 (100)	2 (100)	2 (83) 1 (17)
III-3, number of d/v setae	2/1 (100)	2/1 (100)	2/1 (100)	2/1 (90) 2/0 (10)	2/0 (100)
IV-3, number of d/v setae	2/1 (34) 2/0 (66)	2/1 (25) 2/0 (75)	2/1 (61) 2/0 (39)	2/1 (48) 2/0 (52)	2/0 (100)
III-6, number of d/v setae	4/1 (100)	4/1 (100)	4/1 (82) 3/2 (9) 2/1 (9)	4/1 (100)	4/1 (50) 4/0 (42) 3/1 (8)
IV-6, number of d/v setae	3/1 (97) 3/2 (3)	3/1 (100)	3/1 (100)	3/1 (90) 3/2 (5) 3/0 (5)	3/0 (100)

Basifemur IV. Both variants, with one or no ventral setae, are represented in the material studied.

The *Lobohalacarus weberi* complex includes species and subspecies which are extremely similar in their general facies. Descriptions and discrimination of *Lobohalacarus*, and halacarids in general, are based on external morphological characters. Ultrastructural investigations or data from karyological or molecular genetic studies are lacking until now. Studies in invertebrate taxonomy, using such techniques, proved a number of morphologically almost identical populations to represent complexes of subspecies or species (Grassle and Grassle, 1976; Pietsch and Westheide, 1985; Schlegel *et al.*, 1991; Wood and Backus, 1992; Schmidt and Westheide, 1994).

The external characters in the population of *Lobohalacarus weberi* on Inaccessible Island show some overlap with those of *L. weberi* from the northern hemisphere. Differences in the leg chaetotaxy, the unusual high degree of variability in the Inaccessible population, the geographical distance between northern Europe (with *L. weberi weberi*) and the South Atlantic island in view of low dispersal ability of *Lobohalacarus*, are reasons to distinguish between the populations and to give the specimens from Inaccessible Island the rank of a separate subspecies.

DISPERSAL AND COLONIZATION OF OCEAN ISLANDS

Because of the subsurface way of life and wide geographical distribution of the *Lobohalacarus weberi* complex (records exist from all continents except for Antarctica which has not been studied), one may speculate that these freshwater halacarids belong to an ancient taxon which had already invaded the freshwater of the supercontinent Pangea (Bartsch, 1982). However, the Tristan da Cunha island group and the Hawaiian Islands, both of which have records of *Lobohalacarus*, are of more recent origin. Multiple invasion of a formerly marine ancestor and subsequent speciation and adaption to fresh water is unlikely; thus, *Lobohalacarus* must have been transported to these islands.

Marine, brackish as well as terrestrial species can be spread over long distances through rafting, but *Lobohalacarus*, unable to live but a few hours in seawater, would certainly not survive a transport, drenched with seawater and salt spray, to a distant oceanic island. As documented by Maguire (1963), small aquatic organisms can be dispersed by large animals. *Lobohalacarus weberi*, which can survive in a moist substrate for weeks (Teschner, 1961), may have colonized Inaccessible Island via air, attached to birds or insects which visited continental wells, banks of rivers or groundwater-fed epigean ponds and later rested on Inaccessible Island.

Recent geological investigations by Christie *et al.* (1992) showed that seamounts along submarine ridges once had been islands raised above sea level. These eroded and drowned islands, being considerably older than the present-day volcanic islands in the Galapagos and Hawaiian archipelago, may have been stepping stones for the biota now found on these archipelagos (Christie *et al.*, 1992; Carson, 1992). It is tempting to suppose that the Walvis Ridge provided similar stepping stones and thus eased the colonization of Inaccessible Island.

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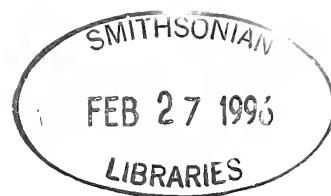
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A comparison of nesting success and nesting habits in some Afrotropical aculeate wasps, with particular reference to nest parasites (Hymenoptera: Sphecidae, Eumenidae)

by

A. J. S. WEAVING
(Albany Museum, Grahamstown)

ABSTRACT

Nest structure, nesting behaviour, nesting success and nest mortality factors of eleven species of aculeate wasps were compared. Seven species nest in pre-existing cavities: *Auplopus femoralis* (Arnold) and *A. vitripennis* Smith (Pompilidae), *Chalybion laevigatum* (Kohl), *Isodontia pelopoeiformis* (Dahlbom) and *I. stanleyi* (Kohl) (Sphecidae), *Tricarinodynerus guerinii* (Saussure) and *Proepipona meadewaldoi* Bequaert (Eumenidae). These were studied using trap-nests. Four species construct aerial mud-nests: *Afreumenes aethiopicus* (Saussure), *Delta hottentottum concinnum* (Saussure) and *Synagris analis* Saussure (Eumenidae) and *Sceliphron spirifex* (L.) (Sphecidae). Study sites were in Natal and the Eastern Cape in South Africa.

Overall nesting success, as measured by the proportions of successful cells, differed in only one of the species. In some cases interspecific success rates differed significantly but inconsistently between localities, due mostly to varying levels of nest parasitism and other mortality factors.

The most important identifiable causes of nest/cell failure were attacks by Miltogramminae (Diptera), Chrysidae and Eulophidae (*Melittobia* sp.) (Hymenoptera) with the addition of *Osprynchotus* sp. (Hymenoptera: Ichneumonidae) in aerial mud-nests. *Ceropales punctulatus* Cameron (Pompilidae) and Leucospidae were very host specific and therefore not of general importance. A number of other taxa including *Stenarella* sp. (Hymenoptera: Ichneumonidae), Mutillidae (Hymenoptera) and Bombyliidae (Diptera) caused mostly low mortality. Endogenous mortality, caused by a combination of unidentifiable factors, was also important. *Chalybion laevigatum* and *T. guerinii* were particularly susceptible to parasitism by Miltogramminae and Chrysidae respectively.

Possible effects of nesting characteristics on nest parasitism are considered in the light of the evidence obtained. Certain characteristics of aerial mud-nests and their influence on parasitism are discussed with reference to nests of *S. spirifex*.

It was concluded that nesting success depended largely on the activities of parasites. The unique nesting habits of each aculeate species provided protection only against specific types of parasites and success was therefore affected by the interaction between nesting habits and the size and species composition of parasite populations.

INTRODUCTION

The enormous diversity in nest structure and nesting behaviour found amongst the aculeate Hymenoptera is extensively documented. However, data on nesting success remain sparse. Success rates, here understood to be the proportions of successful cells, are reported in 11 papers (Rau & Rau, 1916; Taffe & Ittyeipe, 1976; Freeman, 1973, 1977 and 1982; Smith, 1979; Coville & Coville, 1980; Brooke, 1981; Coville & Griswold, 1983 and 1984; Rosenheim, 1987a), and are deducible with varying degrees of certainty from a further 27 out of a selection (not necessarily exhaustive) of 38 papers containing quantitative data; success rates vary between 25 and 100%, averaging 69.1% (Appendix A). However, each of these papers deals with a single species or group of closely related, often congeneric, species.

Thus, direct interspecific comparisons of nesting success are either not available or are limited to closely related species, severely restricting any evaluation of whether nesting habits affect nesting success.

Much of the reported mortality (mean 68.4%, range 30.2 to 98.8%) in nests of aculeate wasps is due to nest parasites and predators (Freeman & Parnell, 1973; Freeman, 1973 and 1982; Taffe & Ittyeipe, 1976; Peckham, 1977; Krombein, 1978; Smith, 1979; Coville & Coville, 1980; Kurczewski & Peckham, 1982; Coville & Griswold, 1983 and 1984; Parker, 1984; Spofford *et al.*, 1986; Rosenheim & Grace, 1987; Rosenheim, 1987a; Weaving, 1989). Many aspects of nesting behaviour and nest structure are therefore interpreted as being antiparasite in function, although this is based on scant supporting data (Rosenheim, 1987a). Relevant literature is listed (not exhaustively) in Appendix A.

If these interpretations are correct, nesting success must be governed largely by interactions between nesting characteristics of aculeates and their predominant parasites. Such interactions have been described for a number of species, mostly ground-nesters from the genera *Anmophila* (Brockmann, 1985; Hager & Kurczewski, 1985; Rosenheim, 1987a and 1989), *Anoplius* (Alm & Kurczewski, 1984), *Bembecinus* (Gess & Gess, 1975), *Bembix* (Evans, 1957, 1966a and 1977), *Centris* (Vinson *et al.*, 1987), *Cerceris* (Linsley & MacSwain, 1956; Evans & Hook, 1982a and 1982b), *Crabro* (Matthews *et al.*, 1979; Evans *et al.*, 1980), *Episyron* (Endo, 1980), *Odynerus* (Hungerford & Williams, 1912), *Oxybelus* (Peckham *et al.*, 1973; Peckham, 1977; Hook & Matthews, 1980), *Paralastor* (Smith, 1978), *Philanthus* (Evans & Lin, 1959; Simonthomas & Simonthomas, 1972; Alcock, 1975; Gwynne, 1981; Evans & O'Neill, 1988), *Podalonia* (O'Brien & Kurczewski, 1982), *Sphex* (Tsuneki, 1963; Brockmann, 1985), *Stictia* (Sheehan, 1984) and *Tachysphex* (Spofford *et al.*, 1986), with a few aerial mud-nesters, *Auplopus* (Weislo *et al.*, 1988), *Eumenes* (Taffe & Ittyeipe, 1976) and *Sceliphron* (Freeman & Ittyeipe, 1976; Freeman, 1982) and species that use pre-existing cavities, *Pachodynerus* (Jayasingh, in Taffe & Ittyeipe, 1976), *Trypargilum* (Krombein, 1979), *Trypoxylon* (Coville & Coville, 1980; Freeman & Ittyeipe, 1993), and bees (Freeman & Ittyeipe, 1993). However, there have been no published attempts to compare nesting success and levels of associated parasitism in a variety of species differing in their nesting habits.

The results of such a comparison are reported here. It was my intention at the outset to include aerial mud-nesting species, those that nest in pre-existing cavities and those that dig burrows in the soil. Unfortunately no ground-nesters were found in sufficient numbers at any locality, so that comparison was of necessity confined to aerial mud-nesters and species that used trap-nests.

METHODS, STUDY PERIOD AND LOCALITIES

DETERMINING CAUSES OF CELL FAILURE

Nest parasites often emerged in the field before nests were collected. Their identification was achieved by comparing residues remaining in the cells with those in cells from which parasites had been reared. Empty puparia and a characteristic "fouling" of cell walls (readily visible in trap-nests) were due to *Mitogramminae* (Fig. 1A). The cocoons of *Chrysididae* (Fig. 1B), *Mutillidae* (Fig. 1C), *Osprynchotus* (Ichneumonidae) (Fig. 1C-D) and *Ceropales* (Pompilidae) (Fig. 1E) were distinguished by means of their appearance, method of emergence by the adult and stage of the cell's development at which they were spun. Large numbers of pupal exuviae more-or-less filling cells or cocoons were characteristic of parasitism by *Melittobia* (2A-B). Adult *Leucospidae* were the only parasites that drilled their way out directly through the side walls of the trap-nests (2C). Such retrospective techniques have been used elsewhere both for aerial mud-nests (Freeman, 1973; Freeman & Parnell, 1973; Taffe & Ittyeipe, 1976) and nests in stem cavities (Danks 1971).

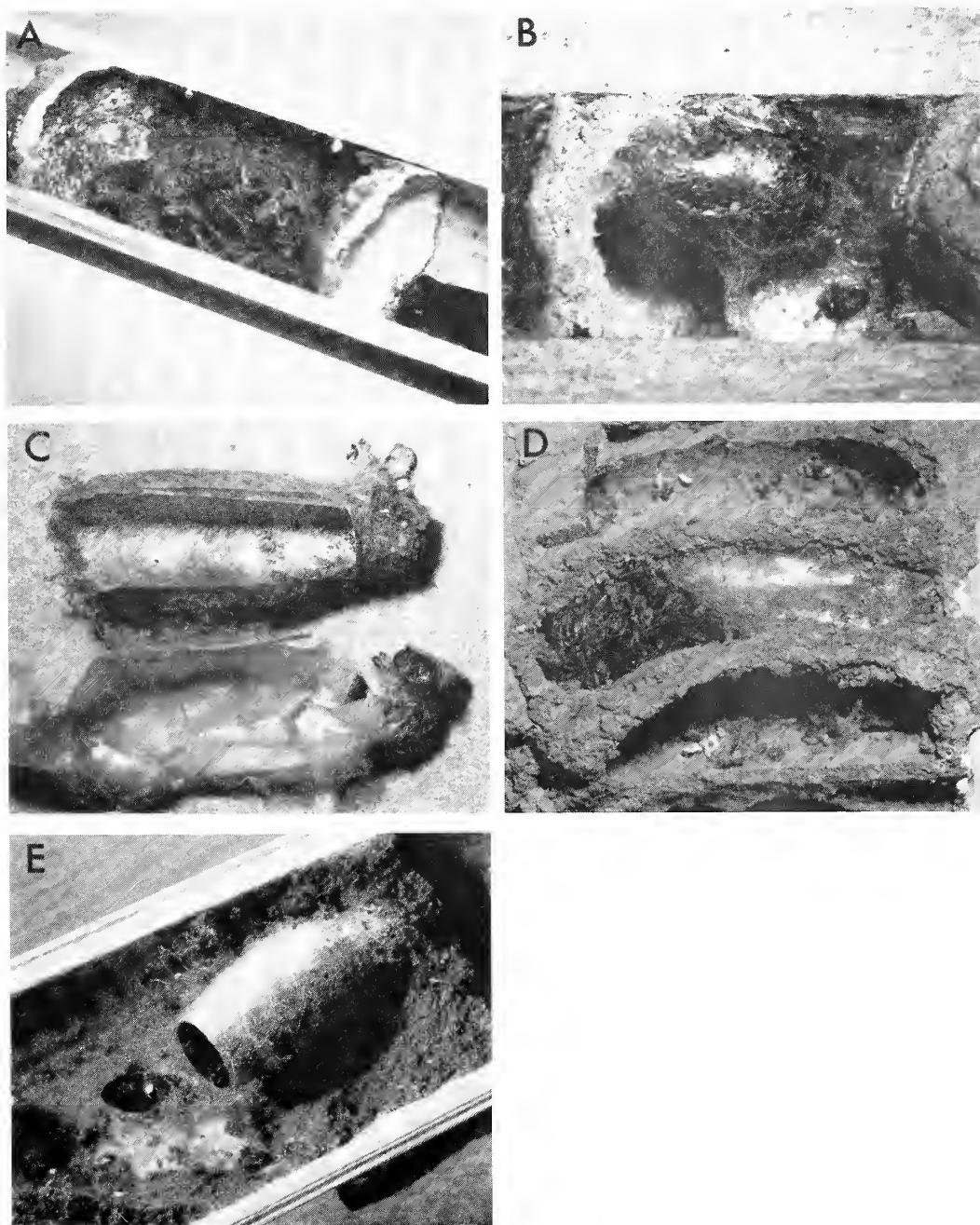


Fig. 1. A - *Chalybion laevigatum* cell parasitised by Miltogramminae, with empty puparia and fouling of cell walls; B - *Tricarindynerus guerintii* cell with chrysidid cocoon; C - *Sceliphron spirifex* cocoons opened to show inner cocoons of mutillid (upper) and *Osprynchotus* (lower); D - *S. spirifex* cell with *Osprynchotus* cocoon (parasitism during larval stage); E - *Ceropales* cocoon with characteristic opening made by adult in *Auplopus vitripennis* cell.

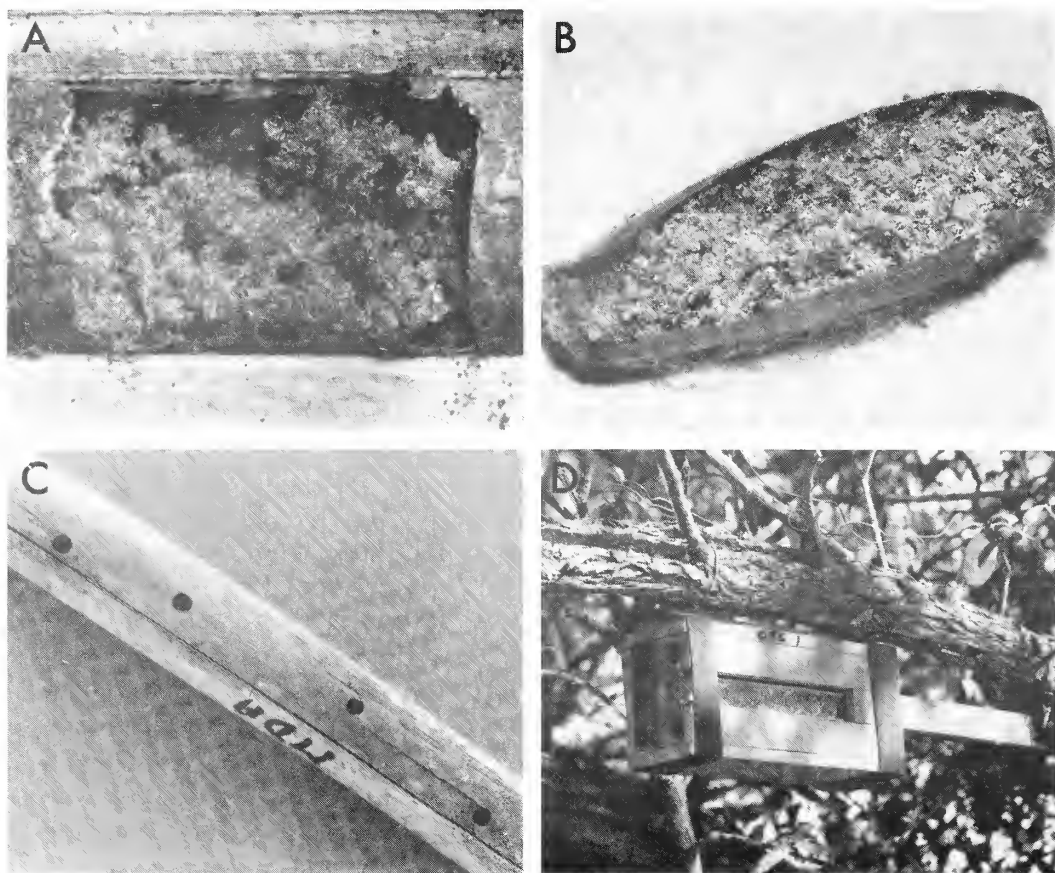


Fig. 2. A - *Tricarinyodnerus guerini* cell and B - *Sceliphron spirifex* cocoon filled with pupal exuviae of *Melitobia*; C - leucospid emergence holes drilled through wall of trap-nest; D - observation trap-nest with cover of one section drawn back to expose window.

AERIAL MUD-NESTS

Disused nests, collected mostly from buildings and road culverts, were dissected to establish the fate of the various cells. Active nests were marked for collection at a future date in order to avoid interfering with parasites and other mortality factors. Observations on behaviour were made whenever possible at active nests.

CAVITY-NESTING SPECIES

Trap-nests, consisting of bundles of three to eight lengths of cane, were suspended from bushes and trees up to 1.8 m above ground and from roof beams of outbuildings with at least one side permanently open. Cavities offered varied from 11 to 245 mm in length and 6 to 21 mm in diameter. More complex trap-nests (Fig. 2D) were also used to allow examination of their contents without

disturbance. Used trap-nests were replaced with new ones at six month intervals at which times observations were made on behaviour at currently active nests. Nests from which the occupants had emerged were opened to record their fate. Nests still occupied were stored and opened at intervals. The times elapsed since completion were not known but nests were categorised according to the stage at which they were opened and whether or not this was followed by further incubation, as follows.

Category 1 - contents emerged or about to emerge; no storage period.

Category 2 - contents consisting of adults and/or pupae; subsequent storage.

Category 3 - contents consisting of various immature stages; subsequent storage.

Category 4 - stored without being opened until emergence.

In the many instances of parasitism by Miltogramminae, Chrysididae, Mutillidae and Leucospidae that were recorded on the basis of remains left behind after their emergence, it was not possible to identify actual species except where dead adult parasites were present. However, as discussed above, the evidence for the different parasite types (i.e. families) was unmistakable. Consequently no differentiation between species in the above families was made in the analyses of levels of parasitism on the assumption that modes of attack were similar within families. In both the Miltogramminae and Chrysididae there was one dominant species, so that any errors due to differences in behaviour must be negligible.

The study started in March 1990 and the final samples were collected in May 1992.

LOCALITIES AND HABITATS

In the Eastern Cape, aerial mud-nests were collected from a road culvert (Table Farm 33°15'S, 26°26'E), the inner walls of a disused fort (Double Drift 33°06'S, 26°47'E), below wooden floors of houses on stilts (Riet River 33°33'S, 27°01'E) and within a suburban house (Grahamstown 33°18'S, 26°31'E). Trap-nests were set up in trees and bushes along watercourses (usually dry) at Thursford (33°11'S, 26°24'E) and Hilton (33°16'S, 26°21'E) and beside a disused sandpit at Hilton.

In Natal, aerial mud-nests were collected from roof beams of buildings at Umlalazi Nature Reserve (28°57'S, 31°47'E), Hluhluwe Game Reserve (28°07'S, 32°03'E), Mkuzi Game Reserve (27°37'S, 32°14'E), Fannies Island (28°06'S, 32°26'E) and False Bay Park (27°58'S, 32°23'E). At Cape Vidal (28°07'S, 32°33'E) they were collected from underneath houses on stilts as well as from roof beams. Trap-nests were attached to external roof beams of the same buildings at the above localities except for Umlalazi Nature Reserve and Cape Vidal. They were also set up in bushes and trees in woodland at Fannies Island, woodland and savannah habitats at Mkuzi Game Reserve and False Bay Park, and forest at False Bay Park and Lake Sibaya (27°23'S, 32°41'E).

SPECIES AND NEST TYPES

AERIAL MUD-NESTERS

Afreumenes aethiopicus (Saussure). Nests were single-celled solitary mud pots, 12-14 mm in diameter with walls approximately 1 mm thick, attached to roof beams, walls and roofing thatch, usually on vertical surfaces (Fig. 3-2). Oviposition was carried out in the empty nest, followed by mass-provisioning with caterpillars. The nest remained open during provisioning and was finally

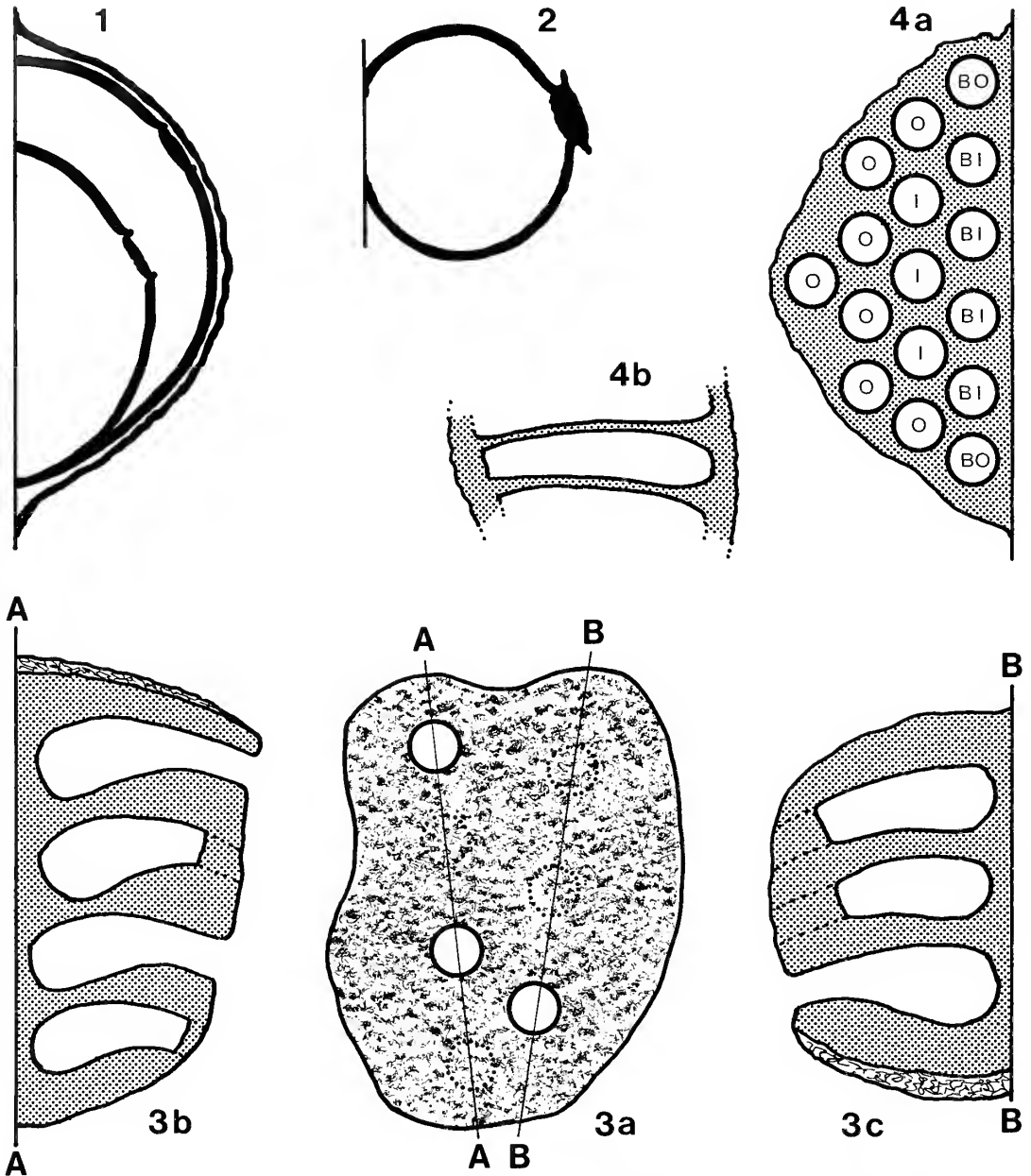


Fig. 3. Sections through nests of the four aerial mud-nesting species. 1 - *Delta hottentottum*, 2 - *Afrumenes aethiopicus*, 3b & c - *Synagris analis*, 4a & b - *Sceliphron spirifex*, indicating cell positions (B-basal, O-outer, I-inner). 3a - frontal view of *Synagris analis* nest.

plugged with mud. The lip around the entrance was not destroyed and there was no additional daubing of the exterior with mud. Females were never observed guarding or otherwise caring for their nests.

Delta hottentottum concinnum (Saussure). Nests were two-celled mud pots, 15-18 mm in diameter with walls approximately 2 mm thick, with broad areas of basal attachment to the substrate (Fig. 3-1). Nests were similarly sited to those of *A. aethiopicus*, also being found on sheltered parts of tree trunks. Oviposition took place immediately on completion of the cell and was followed by mass-provisioning with 2-7 caterpillars. The entrance remained open during provisioning and was finally plugged with mud, some of which was generated by breaking down the surrounding lip using regurgitated water. On completion of the second cell, further mud was collected and applied to the whole nest surface, especially around the base. One timed wasp took 40 min. to build the second cell, 45 min. to provision it with two caterpillars and 75 min. to daub the nest surface. On completion the female abandoned the nest.

All nests of this species found in Natal were of the above structure. In the Eastern Cape, most nests (14/18) were single-celled, often in pairs with the extra daubing covering both cells and making them contiguous. They were usually sited in grooves between bricks on buildings.

Synagris analis Saussure. The substantial mud-nests of this species were multi-celled, sometimes exceeding 0.5 kg in weight, and were attached to roof beams, walls and branches of trees. The structure of a typical nest is shown in Fig. 3-3a-c. A maximum of 17 cells per nest was recorded. Initially thick walls followed by extensive daubing resulted in exceptionally thick cell walls and seals, 12.2 mm (n=30, range 5-22 mm) and 10.3 mm (n=15, range 7-16 mm) respectively. Cells were added progressively upwards, each new cell being fully incorporated into the overall matrix of the nest by daubing before provisioning started. Provisioning with caterpillars was progressive and the cell was sealed once the larva was fully grown, whereupon the next cell was started. Cell entrances were never temporarily sealed and females were always found inside their cells facing outwards, except when away hunting or feeding.

Sceliphron spirifex (L.). The large multi-celled mud-nests of this species (Fig. 3-4a & b) were similarly sited to those of *S. analis*. A maximum of 41 cells in a nest was recorded. Cells were built one by one, each being mass provisioned with spiders before the next was started. Extensive daubing was usually carried out but, in contrast to *S. analis*, only on completed nests. Wall thickness was variable due to an absence of daubing on some nests, which were probably not completed. The thickness of the outer walls of a typical daubed nest ranged from 2.4-4.9 mm (n=7) and the seals 2.9 to 4.9 mm (n=8). No time was spent inside cells by females and entrances remained open during the day until provisioning was complete. Cells were temporarily sealed with mud if provisioning was incomplete at nightfall and were re-opened the following morning.

TRAP-NESTERS

Details of nest structure and aspects of nesting behaviour of *Chalybion laevigatum* (Kohl), *Propeipona meadewaldoi* Bequaert, *Tricarionodynerus guerinii* (Saussure), *Auplopus vitripennis* Smith and *A. femoralis* (Arnold) have already been described (Weaving, 1994a and 1994b). Main nest and behavioural characteristics of these species are summarised alongside the additional species described in Table 1.

Isodontia pelopoeiformis (Dahlbom) and *I. stanleyi* (Kohl). Nest structure and nesting behaviour in these species has been reported from the Eastern Cape by Gess & Gess (1982) and no notable differences were observed in this study. These wasps utilised trap-nests sited in vegetation, and the former species was also found in metal pipes and hollow canes situated horizontally and vertically,

and also in cavities in branches of trees. In nests of *I. pelopoeiformis* partitions were 17.5 mm (n=114, range 5-35 mm) and end seals 65.6 mm (n=71, range 5-125 mm) in thickness. In *I. stanleyi* these measurements were 10.8 mm (n=23, range 5-25 mm) and 54.9 mm (n=13, range 33-102 mm) respectively.

TABLE 1. Summary of main nest and behavioural characteristics of species of aerial mud-nesters and trap-nesters studied.

	Aerial mud-nesters				Trap-nesters						
	Af	Dh	Sy	Ss	Cl	Pm	Tg	Av	lp	Is	Auf
Nest type	SP	DP	MC	MC	L	L	L	L	L	L	DM
No. of cells	1	2	n	n	n	n	n	n	n	n	n
Daubing	-	+	++	+							-
Partition					m*	m	m	M	V	V	
End seal					M*	M	M	VC	VL	VL	
Cell lined					-	-	+	-	-	-	
Vestibular cell					-	+	+	+	-	-	
Superstructure	-	-	-	-	-	-	+	-	-	-	-
Cocoon	F	F	F	D	D	F	F	D	D	D	D
Provisioning	M	M	P	M	M	M/P	M/P	S	M	M	S
Temporary plug	-	-	-	-	-	-	-	-	+	+	-
Guarding	-	-	+	-	-	+	+	+	-	+	+
Nest sharing	-	-	-	-	-	-	-	-	-	-	+

Legend:-

Species	Af = <i>Afreuменes aethiopicus</i> , Auf = <i>Auplopus femoralis</i> , Av = <i>Auplopus vitripennis</i> , Cl = <i>Chalybion laevigatum</i> , Dh = <i>Delta hottentottum</i> , lp = <i>Isodontia pelopoeiformis</i> , Is = <i>Isodontia stanleyi</i> , Pm = <i>Proepipona meadewaldoi</i> , Ss = <i>Sceliphron spirifex</i> , Sy = <i>Synagris analis</i> , Tg = <i>Tricaridynerus guerini</i> .
Nest type	DP = 2-celled mud pots, DM = discrete mud cells in cavity, L = linearly arranged cells in cavity, MC = multicellular composite mud nests, SP = 1-celled mud pots.
No. of cells	n = several.
Daubing	- = nil, + = moderate, ++ = thick.
Partition	m = thin mud, M = thick mud, V = thick vegetable loose.
End seal	M = mud, VC = cemented vegetable, VL = loose vegetable.
Cocoon	D = discrete, F = fills cell as lining.
Provisioning	M = mass, P = progressive, S = single.
	* coated with uric acid ex bird faeces.
Other characteristics	- = negative, + = affirmative.

TABLE 2. Effect of sampling procedure (stage nest opened) on per cent successful emergence of six trap-nesting species, *Tricarinodynerus guerinii* (Tg), *Chalybion laevigatum* (Cl), *Auplopus vitripennis* (Av), *Proepipona meadowaldoi* (Pm) and *Isodontia pelopoeiformis* (Ip).

Species									
Tg		Cl		Av		Pm		Ip	
n=5363		n=918		n=574		n=417		n=364	
Stage	%	Stage	%	Stage	%	Stage	%	Stage	%
2	67.4 ^a	2	51.8 ^a	3	83.4 ^a	2	72.0 ^a	4	77.2 ^a
4	57.1 ^b	3	45.0 ^{ab}	2	82.1 ^a	3	51.2 ^a	2	75.0 ^a
3	47.0 ^c	4	44.0 ^b	1	58.9 ^b	1	34.6 ^b	3	61.1 ^a
1	39.2 ^d	1	36.6 ^b	4	54.8 ^b	4	18.7 ^b	1	26.6 ^b

Possession of common superscripts indicates no significant difference.

TABLE 3. Effect of sampling procedure (stage) on endogenous mortality and inability of adults to emerge in trap-nests of *Tricarinodynerus guerinii*, *Chalybion laevigatum* and *Auplopus vitripennis*.

Endogenous mortality				Blocked emergence			
<i>T. guerinii</i>		<i>C. laevigatum</i>		<i>A. vitripennis</i>		<i>C. laevigatum</i>	
Stage	%	Stage	%	Stage	%	Stage	%
3	28.6 ^a	3	15.8 ^a	4	12.2 ^a	2	8.9 ^a
4	15.7 ^a	2	14.3 ^a	1	6.0 ^b	3	2.3 ^b
1	7.2 ^b	1	8.5 ^b	3	0.0 ^b	4	0.0 ^b
2	6.1 ^b	4	6.9 ^b	2	0.0 ^b	1	0.0 ^b

Possession of common superscripts indicates no significant difference.

EXAMINATION OF THE DATA

SAMPLING PROCEDURE

Chi-square tests were used for each species to assess whether success rates and levels of the various mortality factors were affected by the sampling procedures categorized above (Table 2). Lowest success rates were shown in nests of *T. guerinii* and *I. pelopoeiformis* in category 1 and in nests of *C. laevigatum*, *A. vitripennis* and *P. meadowaldoi* in both categories 1 and 4. Success rates differed between all categories of nests of *T. guerinii* and *C. laevigatum*, although in the latter the differences were less clear cut.

Mortality factors likely to be affected by the sampling procedure were endogenous mortality (due to possible changes in the microclimate in cells), inability to emerge (due to fracturing of cell partitions during opening), and parasitism by *Melittobia* sp. It was found that this parasite can attack at any stage of development. Mortality from Mutillidae, Ichneumonidae, psocids and mites was too low to influence results, whether affected by the sampling procedure or not. Parasitism by

TABLE 4. Effect of sampling procedure (stage) on mortality caused by *Melittobia* in trap-nests of *Tricarinydnerus guerini*, *Chalybion laevigatum* and *Proepipona meadewaldoi*.

<i>T. guerini</i>		<i>C. laevigatum</i>		<i>P. meadewaldoi</i>	
Stage	%	Stage	%	Stage	%
1	29.8 ^a	1	9.5 ^a	4	15.6 ^a
3	9.9 ^b	3	3.6 ^b	1	6.5 ^a
4	6.3 ^b	4	3.4 ^b	3	6.2 ^a
2	6.2 ^b	2	2.7 ^b	2	0.0 ^a

Possession of common superscripts indicates no significant difference.

TABLE 5. Utilisation of data for analysis of success rates and mortality factors.

Species	Data used (stage)	Per cent of whole sample	Per cent of sample due to stage 4
<i>T. guerini</i>	1	46.6	0.0
<i>C. laevigatum</i>	1+4	63.3	3.2
<i>A. vitripennis</i>	1+4	75.0	20.0
<i>P. meadewaldoi</i>	1+4	63.1	7.7
<i>I. pelopoeiformis</i>	1	43.3	0.0

Miltogramminae and Chrysididae is achieved prior to the completion of nests or their sampling and would not therefore have been affected by the sampling.

Endogenous mortality, overall, was not affected by the sampling although there were significant differences between certain categories in nests of *T. guerini* and *C. laevigatum* (Table 3). The inability of adults to emerge from their cells was significantly affected only in nests of *A. vitripennis* and *C. laevigatum* (Table 3).

Mortality caused by *Melittobia* sp. was highest in nests from category 1 of *T. guerini* and *C. laevigatum* (Table 4).

Analysis of success rates was therefore confined to data from category 1 samples which could not be affected by the sampling procedure. Where no significant differences occurred between categories 1 and 4, as with *C. laevigatum*, *A. vitripennis* and *P. meadewaldoi*, the data from these two samples were combined (Table 5). Although some of the individual mortality factors were affected differently in these two categories, category 4 represented only a small proportion of the samples, except in *A. vitripennis* (20%), and would have a negligible effect on success rates. Even with this species, inclusion of data from category 4, with its associated higher mortality due to inability to emerge, merely reduces the success rate from 58.9% for category 1 alone to 57.7% for categories 1 + 4.

DISTRIBUTION OF SAMPLE SIZE

Success rates, levels of nest parasitism and dominance of the different parasites inevitably differed

between localities. It was important therefore to investigate the consistency of interspecific differences between localities by making species comparisons within each locality. Wide variation in sample sizes for species, localities and sample periods limited the range of species that could be compared at each locality. Sample sizes of less than 20 cells were considered unreliable and were discarded.

Species using trap-nests situated in or on buildings were mostly distinct from those in bush sites. *Proecipona meadewaldoi* and the four aerial mud-nesters were largely confined to buildings while both species of *Isodontia* and both *auplopin*es were limited to bush sites, except for a few nests of *I. pelopoeiformis*. Although *C. laevigatum* and *T. guerinii* were primarily found in building sites, numbers using bush trap-nests were sufficiently high for making comparisons between bush sites and building sites.

RESULTS

NESTING SUCCESS - SPECIES COMPARISONS WITHIN LOCALITIES

Results of Chi-square tests on success rates within localities (Table 6) showed significant differences between species at seven of 12 sites in/on buildings. Significant differences between trap-

TABLE 6. Per cent success rates of adequately sampled species at sites in buildings compared within localities.

FBA		FBG		FBR		FI		FIC	
Cl	60.3 ^a	Sy	45.9^a	Cl	41.5 ^a	Dh	49.5^a	Af	63.5^a
Tg	53.6 ^a	Tg	28.6 ^b	Tg	34.4 ^a	Ss	29.9^b	Tg	62.8 ^a
Pm	51.4 ^a	Cl	20.1 ^b	Pm	30.7 ^a	Af	25.0^b		
		Pm	20.0 ^b	Af	30.0^a				
		Ss	5.0^c	Ss	16.4^b				
FIG		MK		MKB		HL		UL	
Tg	65.9 ^a	Af	37.9^a	Tg	38.0 ^a	Af	52.8^a	Af	81.2^a
Pm	46.1 ^a	Ss	26.7^a	Cl	31.0 ^a	Ss	48.9^a	Sy	74.2^a
Cl	0.0 ^b					Dh	45.2^a	Dh	26.7^b
								Ss	14.7^b
CV		GT (Cape)							
Ss	89.6^a	Ss	61.0^a						
Af	57.1^b	Dh	26.3^b						

Species abbreviations as in Table 1.

Locality abbreviations as follows:-

FBA/FBG/FBR - ablution block/garage/rustic huts at False Bay Park; **FI/FIC/FIG** - rest huts/ablution block/garage at Fannies Island; **MK/MKB** - various outbuildings/field offices at Muzi Game Reserve; **HL/UL/CV** - outbuildings at Hluhluwe Game Reserve/Umlalazi Nature Reserve/Cape Vidal; **GT** - Grahamstown suburban house.

Possession of common superscripts signifies no significant difference.

Species in bold are aerial mud-nesters.

nesting species occurred only at FIG where *C. laevigatum* achieved zero success. Where trap-nesters and aerial mud-nesters occurred together, *S. spirifex* was the least successful (at FBR and FBG) and *S. analis* the most successful (at FBG). *Synagris analis* was again more successful than *S. spirifex* at UL. *Delta hottentottum* was either more or similarly successful compared with *S. spirifex* at three Natal sites, but was significantly less successful at GT in the Cape. At four of six localities where *S. spirifex* and *A. aethiopicus* could be compared, the latter was more successful, significantly so at two. However, at Cape Vidal the reverse was true.

TABLE 7. Per cent success rates of adequately sampled species from bush sites compared within localities.

FBT		FIP		MKH		MKM		MKN	
Auf	75.3 ^a	Auf	69.7 ^a	Av	82.9 ^a	Av	67.1 ^a	Cl	69.2 ^a
Av	55.5 ^b	Av	61.1 ^a	Ip	76.9 ^a	Auf	41.7 ^b	Tg	63.4 ^a
Cl	42.8 ^b			Auf	44.8 ^b			Av	58.8 ^a
MKO		SIB		H (Cape)					
Auf	67.6 ^a	Av	71.4 ^a	Is	57.9 ^a				
Ip	56.0 ^{ab}	Ip	9.8 ^b	Ip	0.0 ^b				
Tg	36.4 ^{bc}								
Av	31.6 ^c								

Species abbreviations as in Table 1.

Locality abbreviations as follows:-

FBT/FIP - False Bay Park/Fanies Island woodland;

MKH/MKM/MKN/MKO - savannah/woodland/forest/woodland at Mkuzi Game Reserve;

SIB - Lake Sibaya forest;

H (Cape) - trees/bushes bordering sandpit and watercourse.

Possession of common superscripts signifies no significant difference.

Similar tests on data from bush sites (Table 7) showed significant differences between species at six of eight sites. However, no consistent trends were discernible for any species. For instance, *A. vitripennis* was most successful at MKM and SIB but among the least so at MKO and FBT; *A. femoralis* was more successful than *A. vitripennis* at FBT and MKO but less so at MKH and MKM.

Thus, intra-locality success rates differed significantly at thirteen of the 20 localities with adequately sized samples (Tables 6 and 7). Whilst there were certain trends in relative success rates, actual levels for individual species showed much heterogeneity between localities (Fig. 4).

Collectively, trap-nesting species were more successful in bush sites than in buildings, 54.8 and 38.3% respectively ($t=3.83$ $df=7$ $p<0.01$ with arcsin transformation). Trap-nesters in buildings did not differ significantly from aerial mud-nesters in their collective success rates, 38.3 and 43.3% respectively ($t=1.53$ $df=8$ $p>0.10$ with arcsin transformation).

NESTING SUCCESS AND MAIN MORTALITY FACTORS

INTER-LOCALITY COMPARISONS OF TRAP-NESTING SPECIES

A simultaneous assessment of host species and localities in relation to overall nesting success

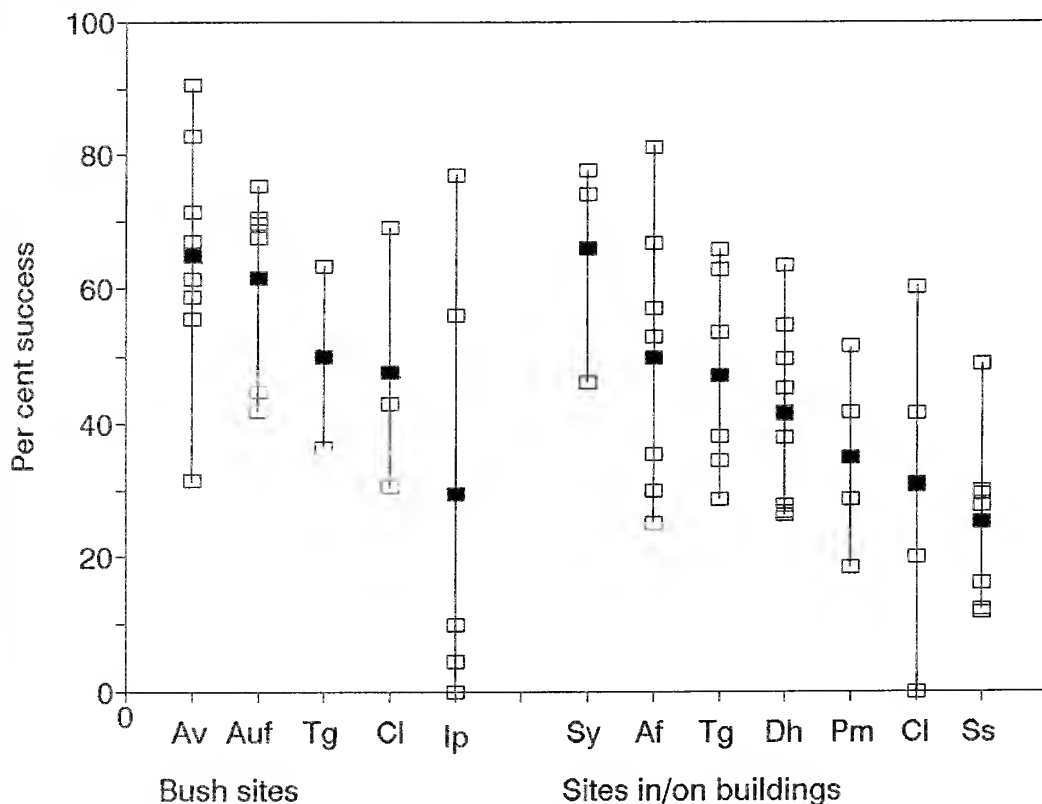


Fig. 4. Interlocality variation in nesting success in six trap-nesting and four aerial mud-nesting wasps. Mean success is shown with solid squares.

or mortality due to particular parasites was not possible since locality sets differed for each host as a result of inadequate sample sizes. Instead, data from sites with samples exceeding 20 cells were compared separately for each species using Chi-square tests. Localities marked with * in Tables 8 and 9 had relatively small samples (<50 cells) which are therefore less reliable.

Chalybion laevigatum. Nesting success varied from zero to 69.2% depending largely on levels of parasitism by Miltogramminae and *Melittobia* (Table 8, Fig. 5). Exceptionally high endogenous mortality contributed to the zero success at FIG but in this case the sample size was minimal. The high levels of attack by Miltogramminae and *Melittobia*, and resultant low success rate at FBG, are probably attributable to the long-standing presence at this locality of a large population of *T. guerinii*, with its associated parasites, nesting in a cane partition.

Tricarinodynerus guerinii. A wide range in nesting success was again demonstrated, attributable in this case mainly to varying levels of parasitism by Chrysididae, *Melittobia* and unknown factors (Table 8, Fig. 5). It is noteworthy that, again, success was lowest and parasitism by *Melittobia* highest at FBG.

Proepipona meadewaldoi. Varying success rates appeared to be linked to levels of endogenous mortality and parasitism by Chrysididae (Table 8, Fig. 5). Parasitism by Miltogramminae was high

TABLE 8. Success rates and mortality factors in trap-nesters mostly in/on buildings.

		Per cent success and parasitism								
Site	n	SE	EM	DP	CH	MU	OS	IC	MT	?F
<i>Chalybion laevigatum</i>										
MKN	52	69.2 ^a	1.9	9.6	13.5	0.0	3.8	0.0	0.0	1.9
FBA	73	60.3 ^a	5.5	24.6	5.5	0.0	0.0	0.0	0.0	2.7
FBT	21	42.8 ^{ab}	4.8	33.3	0.0	0.0	0.0	19.0	0.0	0.0
FBR	147	41.5 ^b	8.2	28.6	6.8	0.7	2.0	0.7	2.7	3.4
MKB*	29	31.0 ^{bc}	6.9	41.4	0.0	3.4	0.0	0.0	13.8	3.4
MKO*	36	30.5 ^c	8.3	16.7	27.8	2.8	2.8	0.0	0.0	2.8
FBG	184	20.1 ^c	8.1	47.3	0.0	0.4	0.0	0.5	21.2	0.0
FIG*	21	0.0 ^d	33.3	19.0	0.0	0.0	0.0	4.8	33.3	4.8
<i>Tricarinodysnerus guerinii</i>										
FIG	129	65.9 ^a	4.6	0.0	10.8	0.0	0.0	0.0	9.3	4.6
MKN	82	63.4 ^{ab}	3.6	2.4	20.7	0.0	0.0	0.0	8.5	1.2
FIC	113	62.8 ^{ab}	6.2	0.9	19.5	0.0	0.0	0.0	8.0	0.9
FBA	420	53.6 ^b	5.0	3.6	24.5	0.9	0.0	0.0	9.8	1.7
MKB	450	38.0 ^c	6.0	0.2	22.2	0.4	0.0	0.4	24.7	3.8
MKO*	22	36.4 ^{cd}	4.5	0.0	36.4	4.5	0.0	0.0	0.0	13.6
FBR	61	34.4 ^{cd}	3.3	11.5	32.8	0.0	0.0	0.0	0.0	18.0
FBG	1197	28.6 ^d	7.8	6.3	6.3	0.1	0.0	0.0	47.4	0.7
<i>Proepipona meadewaldoi</i>										
FBA*	35	51.4 ^a	5.7	22.9	0.0	2.9	0.0	0.0	0.0	2.9
FIG*	36	41.6 ^{ab}	25.0	2.8	0.0	0.0	0.0	0.0	5.5	8.3
FBR	133	28.6 ^b	25.6	18.8	7.5	0.0	0.0	0.0	10.5	3.8
FBG*	38	18.4 ^b	28.9	2.6	10.5	0.0	0.0	5.3	10.5	2.6

Site abbreviations as in Tables 6 and 7, bush sites in bold.

SE - successful cells; **EM** - endogenous mortality; **DP** - miltogramminae; **CH** - Chrysididae; **MU** - Mutillidae; **OS** - *Osprynchotus* sp.; **IC** - *Stenarella* sp.; **MT** - *Melittobia*; **?F** - fate unknown.

Localities in bold are in bush sites.

Localities marked * are inadequately sampled (<50 cells).

Possession of common superscripts indicates no significant difference.

at FBA and FBR but the impact was reduced by low or zero levels of the above two factors at FBA. Lowest success rates again occurred at FBG.

Auplopus vitripennis. Endogenous mortality was the most consistent factor affecting nesting success (Table 9, Fig 5). Levels of attack by the various nest parasites varied erratically between localities but higher mortality from unknown causes, Leucospidae and/or Ceropales was responsible for the significantly reduced success rates at FBT and MKO.

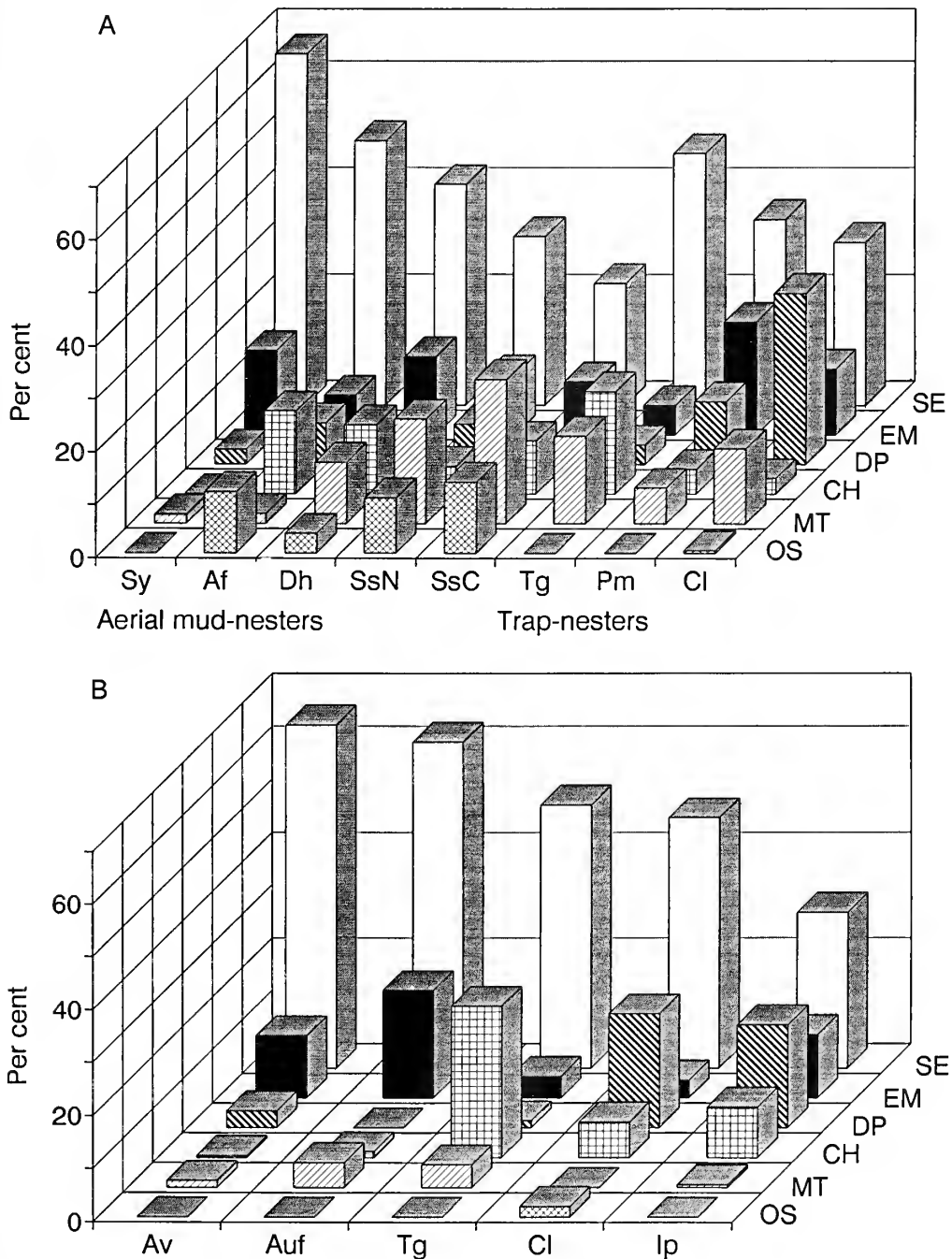


Fig. 5. Relative impact of five main mortality factors on nesting success in A - trap-nesters and aerial mud-nesters in/on buildings and B - trap-nesters in bush sites.

TABLE 9. Success rates and mortality factors in trap-nesters confined to bush sites.

Site	n	Per cent success and parasitism									
		SE	EM	DP	CH	MU	LE	CE	IC	MT	?F
<i>Auplopus vitripennis</i>											
FBM*	21	90.5 ^a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MKH*	35	82.9 ^a	11.4	0.0	0.0	0.0	0.0	0.0	0.0	2.9	2.9
SIB*	21	71.4 ^{ab}	14.3	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MKM	79	67.1 ^{ab}	19.0	0.0	0.0	6.3	0.0	0.0	0.0	1.3	0.0
FIP	140	61.4 ^{ab}	10.0	0.0	1.4	2.1	2.2	6.5	0.0	0.7	7.1
MKN*	34	58.8 ^b	14.7	8.8	0.0	0.0	0.0	0.0	0.0	5.9	0.0
FBT*	45	55.5 ^b	8.9	0.0	0.0	2.2	0.0	0.0	2.2	0.0	15.5
MKO	79	31.6 ^c	15.2	1.3	0.0	2.5	13.9	11.4	0.0	0.0	1.3
<i>Isodontia pelopoeiformis</i>											
MKH*	26	76.9 ^a	7.7	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MKO*	25	56.0 ^a	4.0	24.0	8.0	0.0	8.0	0.0	0.0	0.0	0.0
SIB*	41	9.8 ^b	2.4	2.4	9.8	9.9	68.3	0.0	0.0	2.4	4.9
TCape*	23	4.3 ^b	26.1	17.4	8.7	0.0	0.0	0.0	0.0	0.0	34.8
HCape*	43	0.0 ^b	18.6	37.2	20.9	0.0	0.0	0.0	0.0	0.0	9.3
<i>Isodontia stanleyi</i>											
FIP +											
MKH*	18	83.3 ^a	5.5	5.5	0.0	0.0	0.0	0.0	0.0	5.5	0.0
HCape*	19	57.9 ^a	15.8	5.3	10.5	0.0	0.0	0.0	0.0	0.0	5.3
<i>Auplopus femoralis</i>											
FBT	77	75.3 ^a	10.4	0.0	1.3	0.0	0.0	0.0	0.0	0.0	9.1
MKN*	17	70.6 ^{ab}	23.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9
FIP*	33	69.7 ^{ab}	12.1	0.0	0.0	9.1	0.0	0.0	0.0	0.0	9.1
MKO*	34	67.6 ^{ab}	29.4	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0
MKH*	29	44.8 ^b	24.1	0.0	0.0	17.2	0.0	0.0	0.0	10.3	0.0
MKM*	36	41.8 ^b	22.2	0.0	5.5	8.3	0.0	0.0	0.0	16.7	2.8

Site abbreviations as in Tables 6 and 7.

SE - successful cells; **EM** - endogenous mortality; **DP** - miltogramminae; **CH** - Chrysididae; **MU** - Mutillidae; **LE** - Leucospidae; **CE** - Ceropales; **IC** - Stenarella sp.; **MT** - Melittobia; **?F** - fate unknown.

Localities marked * are inadequately sampled (<50 cells).

Possession of common superscripts indicates no significant difference.

Isodontia pelopoeiformis. Leucospidae were responsible for a substantial and significant reduction in nesting success at one locality in Natal (Table 9). Otherwise the main mortality factor was Miltogramminae (Fig. 5). Very low success rates were also recorded at both Cape sites due to high levels of endogenous mortality, Miltogramminae, Chrysididae and/or unknown factors.

Isodontia stanleyi. This species was sampled at only two of the sites in Natal and sample sizes were well below the minimum of 20 cells. However, at site H in the Cape it was 19. A comparison was therefore made of the combined Natal sample (18 cells) with the Cape sample. There was no significant difference in nesting success between the two areas (Table 9). Endogenous mortality and parasitism by Chrysididae appeared to be greater at the Cape site but much larger samples are required for this species.

Auplopus femoralis. Success rates were relatively high at four of six localities but only one of these (FBT) differed significantly from the remaining two less successful ones, MKH and MKM (Table 9). There were no records of parasitism by Miltogramminae, Leucospidae or Ichneumonidae. Endogenous mortality was the main cause of failure at all localities (Fig. 5). Mutillidae, *Melittobia* and unknown factors reduced success only at some localities.

INTER-LOCALITY COMPARISONS OF AERIAL MUD-NESTING SPECIES

Afreumenes aethiopicus. Success rates in Natal varied from 25.0 to 81.2% largely due to fluctuating levels of attack by the three main nest parasites, Miltogramminae, Chrysididae and the ichneumonid *Osprynchotus* sp. and, to a lesser extent, endogenous mortality (Table 10, Fig. 5). Mutillidae were important at only one locality. Data from a well separated locality, Malindi in East Africa, showed similar trends to those from South Africa.

Delta hottentottum concinnum. Nesting success at four Natal localities was significantly lower than at FIC due mainly to increased levels of attack by the two principal nest parasites, Chrysididae and *Melittobia* (Table 10, Fig. 5). Endogenous mortality was again a consistent cause of failure. Mortality factors and success rates at GT in the Cape did not differ from those in Natal except for FIC.

Sceliphron spirifex. The multi-celled aerial mud-nests of this species may contain up to 40 or more cells. Consequently interlocality comparisons were limited to those localities with samples from an arbitrary minimum of 10 nests to increase the reliability of the results. Nesting success varied from 11.8 to 48.9% (Table 10). Very high levels of parasitism by *Melittobia* (Fig 5) were responsible for the success rates being significantly lowest at RR and MKB. Varying combinations of endogenous mortality, Miltogramminae, Chrysididae, *Osprynchotus*, *Melittobia* and mortality from unknown causes also significantly reduced success at a further three localities compared with that at HL. All factors with the exception of Mutillidae and *Stenarella* were responsible for significant (>10%) mortality at one or more of the localities. Data from Malindi (East Africa) showed no notable deviations from the pattern observed in Natal and Eastern Cape. Sample size was, however, inadequate for inclusion in the analysis.

Synagris analis. Sample sizes were small for this species and it was not possible to apply the minimum of 10 nests for interlocality comparisons. Chi-square tests were therefore carried out using data from localities with more than one nest, namely FBG, FIG and UL with 9, 4 and 4 nests respectively, in order to provide some comparison with *S. spirifex*. Nesting success was significantly reduced at FBG due to Miltogramminae and *Melittobia* which were not recorded from nests of this species at the other sites, and to a relatively high level of attack by Mutillidae (Table 10). Thus, apart from FBG where success rates may have been affected by an abnormally high parasite population emanating from nests of *T. guerini*, *S. analis* appeared to enjoy a high level of nesting success, Mutillidae being the main parasite.

OVERALL NESTING SUCCESS

Differing pressures from the various mortality factors between localities were primarily

TABLE 10. Success rates and mortality factors in aerial mud- nesting species.

Site	n	Per cent success and parasitism								
		SE	EM	DP	CH	MU	OS	IC	MT	?F
<i>Afreumenes aethiopicus</i>										
UL*	16	81.2 ^a	6.2	0.0	0.0	0.0	6.2	0.0	6.2	0.0
CV	175	57.1 ^{ab}	6.8	1.1	18.3	0.6	6.3	0.0	2.8	5.1
HL*	36	52.8 ^{abc}	11.1	5.5	2.8	13.9	11.1	0.0	0.0	2.8
FIG*	17	35.3 ^{bc}	0.0	5.9	41.2	5.9	5.9	0.0	0.0	5.9
FBR	70	30.0 ^c	7.1	21.4	0.0	4.3	27.1	0.0	1.4	8.6
FI*	16	25.0 ^c	12.5	12.5	31.2	0.0	12.5	0.0	0.0	6.2
MI#	30	66.7	0.0	0.0	10.0	3.3	10.0	0.0	3.3	0.0
<i>Delta hottentottum</i>										
FIC	74	63.5 ^a	14.9	0.0	8.1	1.3	5.4	0.0	1.3	4.0
MKE*	22	54.5 ^{ab}	13.6	4.5	0.0	18.2	4.5	0.0	0.0	4.5
FI	103	49.5 ^{ab}	14.6	1.0	10.7	2.9	7.8	0.0	1.0	7.8
HL*	42	45.2 ^{ab}	7.1	7.1	2.4	4.8	7.1	0.0	23.8	2.4
FBG*	48	41.7 ^b	6.2	4.2	10.4	4.2	2.1	0.0	16.7	10.4
MK	58	37.9 ^b	13.8	6.9	6.9	1.7	6.9	0.0	13.8	10.3
FIG*	18	27.8 ^b	27.8	5.5	22.2	0.0	0.0	0.0	0.0	5.5
UL*	30	26.7 ^b	13.3	0.0	20.0	0.0	0.0	0.0	36.7	3.3
GT*	19	26.3 ^b	21.0	0.0	36.8	0.0	0.0	0.0	10.5	5.3
<i>Sceliphron spirifex</i>										
HL	309	48.9 ^a	8.1	4.5	10.0	1.3	14.6	0.0	4.8	6.1
FI	163	29.9 ^b	15.6	16.9	3.9	0.6	10.4	0.0	13.0	2.6
DD	153	29.4 ^b	17.6	0.0	9.1	0.0	20.9	0.0	0.6	17.0
TF	220	27.7 ^b	9.1	2.3	19.1	0.4	5.9	0.0	18.2	10.9
MKB	178	16.3 ^c	10.1	1.1	1.7	5.1	6.2	0.0	41.6	12.9
RR	279	11.8 ^c	3.6	0.4	1.8	0.0	13.3	0.0	63.1	4.7
MI#	41	12.2	12.2	9.7	9.7	0.0	19.5	0.0	7.3	24.4
<i>Synagris analis</i>										
FIG*	18	77.8 ^a	5.5	0.0	0.0	11.1	0.0	0.0	0.0	5.5
UL*	31	74.2 ^a	25.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FBG*	61	45.9 ^b	16.4	8.2	0.0	14.7	0.0	0.0	4.9	8.2

Locality abbreviations as in Tables 6 and 7.

Success and parasite abbreviations as in Tables 8 and 9.

MI# Data from Malindi not included in analysis.

Localities marked * are inadequately sampled (<50 cells or <10 multi-celled nests).

Possession of common superscripts indicates no significant difference.

TABLE 11. Results of t-tests on overall per cent success rates using arcsin transformation.

Species	Nest type	Mean % success (arcsin)	
Sites in/on buildings:			
<i>Synagris analis</i>	AM	54.6 ^a	
<i>Afreumenenes aethiopicus</i>	AM	43.5 ^a	
<i>Tricarinodynerus guerinii</i>	TN	43.3 ^a	c
<i>Delta hottentottum</i>	AM	41.2 ^a	
<i>Proepipona meadewaldoi</i>	TN	35.9 ^a	
<i>Sceliphron spirifex</i> (N)	AM	33.8 ^a	d
<i>Chalybion laevigatum</i>	TN	31.5 ^a	c
Bush sites:			
<i>Auplopus vitripennis</i>	TN	54.3 ^a	
<i>Auplopus femoralis</i>	TN	51.9 ^a	
<i>Tricarinodynerus guerinii</i>	TN	44.9 ^a	c
<i>Chalybion laevigatum</i>	TN	43.5 ^a	c
<i>Isodontia pelopoeiformis</i> (N)	TN	42.7 ^a	e
Cape sites:			
<i>Sceliphron spirifex</i> (C)	AM/B	28.2 ^a	d
<i>Isodontia pelopoeiformis</i> (C)	TN/O	7.6 ^b	e

AM = aerial mud nest; TN = trap-nest; B = in/on buildings; O = bush sites; (C) = Cape sites; (N) = Natal sites.

Possession of common superscripts within columns signifies no significant difference. Results of certain species analyses are indicated in superscript columns c, d and e.

responsible for the intra-specific variations in nesting success. In order to assess whether there were overall differences in interspecific success rates, data from the relevant localities were combined and subjected to t-tests (Table 11). No species in either bush or building sites in Natal differed significantly from any other. At Cape sites, *I. pelopoeiformis* was significantly less successful than *S. spirifex*. Species common to both Cape and Natal sites (*S. spirifex* and *I. pelopoeiformis*) and those common to sites in buildings and bush sites in Natal (*T. guerinii* and *C. laevigatum*) also showed no significant differences in success rate. Thus, with the one exception at Cape sites, species did not differ overall in nesting success when considered over the range covered by the study.

While recognising the need for more data from localities from as many parts of each species' distribution as possible, the present data indicate that differences in nest structure and nesting behaviour do not result in consistent differences in nesting success. They may, however, affect levels of attack by specific nest parasites and mortality due to other factors as indicated in Table 12. The relative importance of the various mortality factors varies markedly between species (Fig. 5).

EFFECTS OF NEST AND BEHAVIOURAL CHARACTERISTICS ON MORTALITY FACTORS

The main nest structural and behavioural characteristics of the species studied are summarised

TABLE 12. Interspecific comparisons of mean success rates and mortality factors.

Species	Pcr cent success and parasitism										
	SE	EM	DP	CH	MU	LE	CE	OS	IC	MT	?F
Trap-nests in bush sites											
ls	70.6	10.6	5.4	5.2	0.0	0.0	0.0	0.0	0.0	2.2	2.6
Av	64.9	11.7	3.0	0.2	1.6	2.0	2.2	0.0	0.3	1.3	3.3
Auf	61.6	20.3	0.0	1.1	5.8	0.0	0.5	0.0	0.0	4.5	4.5
Tg	49.9	4.0	1.2	28.5	2.2	0.0	0.0	0.0	0.0	4.2	7.4
Cl	47.5	3.3	21.4	6.7	0.0	0.0	0.0	1.9	9.5	0.0	0.9
lp	29.4	11.8	19.3	9.5	2.0	15.3	0.0	0.0	0.0	0.5	9.8
Trap-nests in/on buildings											
Tg	47.2	5.5	3.7	19.3	0.2	0.0	0.0	0.0	0.1	16.5	4.9
Pm	35.0	21.3	11.8	4.5	0.7	0.0	0.0	0.0	1.3	6.6	4.4
Cl	30.6	12.4	32.2	2.9	0.9	0.0	0.0	0.4	1.2	14.2	2.9
Aerial mud-nests in/on buildings											
Sy	66.0	15.9	2.7	0.0	8.6	0.0	0.0	0.0	0.0	1.6	4.6
Af	49.7	7.3	7.7	15.6	4.1	0.0	0.0	11.5	0.0	1.7	1.7
Dh	41.4	14.7	3.2	13.0	3.7	0.0	0.0	3.7	0.0	11.5	5.9
Ss (N)	31.7	11.3	7.5	5.2	2.3	0.0	0.0	10.4	0.0	19.8	7.2
Ss (C)	23.0	10.1	0.9	10.0	0.1	0.0	0.0	13.4	0.0	27.3	10.9

Species abbreviations as in Table 1.

Success and parasite abbreviations as in Tables 8 and 9.

in Table 1 for comparison with the impact of nest parasites on their hosts. The more important parasites and their recorded hosts are listed in Table 13.

MILTOGRAMMINAE

Amobia africa Curran was the most commonly recorded species. *Senotainia albifrons* occurred in much lower numbers, and any error resulting from grouping the two species together in the analyses will be negligible. The discussion below therefore refers mainly to *A. africa*. The apparently more restricted range of hosts of *S. albifrons* (Table 13) may be at least partly due to the small sample. However, these records are of particular interest since this species has apparently never been reared from an Afrotropical host, and Palearctic records are from soil-nesting sphecids (Pape, pers. comm.) compared with trap-nesting species parasitised in this study.

Bush sites. Levels of parasitism were compared using t-tests. Data from all samples were used on the assumption that attack by Miltogramminae was not affected by the stage at which trap-nests were sampled. At Natal sites *C. laevigatum* suffered significantly higher mortality than *A. vitripennis*, *T. guerini* and *A. femoralis* (Table 14). Parasitism of *C. laevigatum* and *I. pelopoeiformis* (at both Natal and Cape sites) did not differ significantly. These species differ in several nesting characteristics (Table 1) but composition of cell partitions and end seals, cell linings, the presence or absence of vestibular cells and cocoon types are probably irrelevant, since larviposition by Miltogramminae occurs during cell provisioning. The composition of cell partitions could, however, affect migration of maggots between cells.

TABLE 13. Host selection by species of principal parasites

Parasite	Bush sites				Sites in buildings						
	Av	Auf	Ip	Is	Cl*	Tg*	Pm	Af	Dh	Ss	Sy
MILTOGRAMMINAE											
<i>Amobia africa</i>	+	-	+	-	+	+	+	+	-	-	-
<i>Senotainia albifrons</i>	-	-	+	+	+	-	-	-	-	-	-
CHRYSIDIDAE											
<i>Chrysis</i> sp.											
<i>wahlbergi</i> grp	+	+	-	-	+	+	+	-	+	+	+
<i>oculata</i> grp	-	-	-	-	-	-	-	-	+	-	-
<i>lincea</i> grp	-	-	-	-	-	-	-	-	-	+	-
<i>smaragdula</i> grp	-	-	-	-	-	-	-	-	-	-	-
<i>succincta</i> grp	-	-	+	+	-	-	-	-	-	-	-
<i>Stilbum cyanurum</i>	-	-	-	-	-	-	-	+	+	-	-
<i>Primeuchroeus</i> sp.											
<i>ghilianii</i> grp	-	+	-	-	-	-	-	-	-	-	-
MUTILLIDAE											
<i>Stenomutilla syrinx</i>	-	-	-	-	+	+	+	-	+	+	+
<i>Dolichomutilla sycorax</i>	-	-	-	-	-	+	-	-	-	+	+
<i>D. heterodonta</i>	-	+	-	-	-	+	-	+	-	-	-
<i>Antennotilla</i> sp.	+	+	+	-	-	-	-	-	-	-	-
ICHNEUMONIDAE											
<i>Osprynchotus</i> sp.	-	-	-	-	+	-	+	+	+	+	-
<i>Stenarella</i> sp.	+	-	-	-	+	+	-	-	-	-	-
LEUCOSPIDAE											
<i>Leucospis varicollis</i>	+	-	-	-	-	+	-	-	-	-	-
<i>L. ornata</i>	-	-	-	-	-	+	-	-	-	-	-
<i>L. fuelleborniana</i>	-	-	+	-	-	-	-	-	-	-	-
POMPILIDAE											
<i>Ceropales punctulatus</i>	+	-	-	-	-	-	-	-	-	-	-
EULOPHIDAE											
<i>Melittobia</i> sp.	+	+	+	+	+	+	+	+	+	+	+

Species abbreviations as in Table 1.

**C. laevigatum* and *T. guerinii* used trap-nests in both bush and building sites.

! indicates parasitism recorded only from building sites.

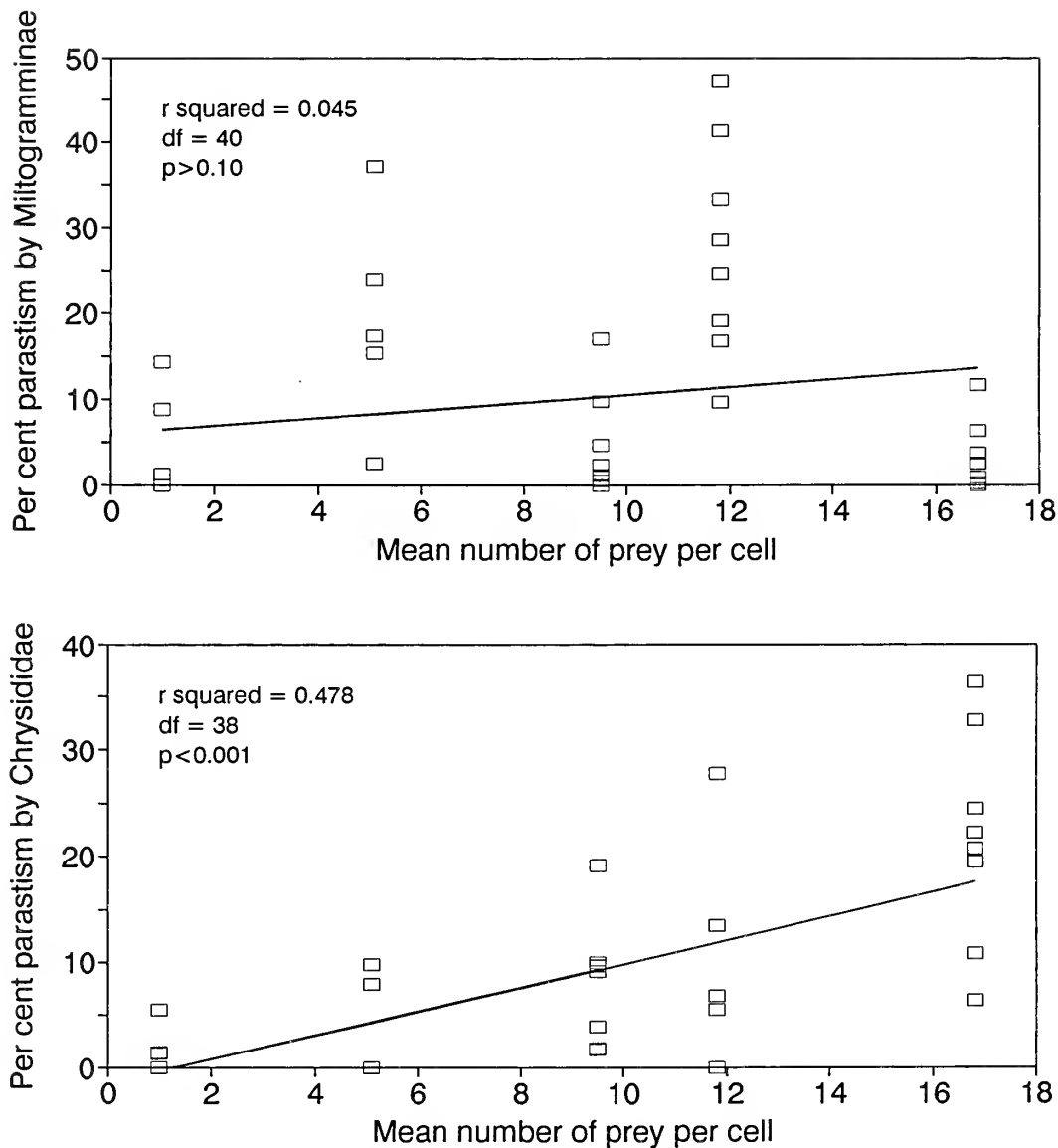


Fig. 6. Relationship between number of prey per cell and levels of parasitism by Miltogramminae and Chrysididae.

Characteristics that could influence attack by Miltogramminae are the use of temporary nest plugs, nest guarding and methods of provisioning. The time required to provision a cell completely will in many cases be longer in species using greater numbers of prey. This, combined with the greater number of visits made to respective nests, provides more opportunities for larviposition by Miltogramminae. However, the correlation between levels of parasitism and mean numbers of prey

TABLE 14. Results of t-tests on levels of parasitism due to *Miltogramminae*.

Species	% parasitism (arcsin)	Species pair	t-tests			Prey per cell		
	t		df	p	mean	range	n	
Trap-nesters in bush sites:								
Ip(C)	31.1 ^a	Cl/Av	3.31	9	<0.01	5.1	2 - 14	13
Cl	25.8 ^a	Ip(C)/Ip(N)	1.17	3	>0.1	11.8	4 - 27	34
Ip(N)	20.4 ^{ab}	Ip(N)/Tg	1.66	3	>0.1			
Av	7.3 ^b	Ip(N)/Av	2.22	9	>0.05	1.0		
Tg	7.3 ^b					16.8	5 - 35	55
Auf	0.0 ^c					1.0		
Trap-nesters and aerial mud-nesters in/on buildings:								
Cl	34.3 ^a	Tg/Pm	1.67	8	>0.05	11.8	4 - 27	34
Pm	18.0 ^b	Cl/Pm	2.74	7	<0.05		no data	
Af	14.8 ^b	Ss(C)/(N)	1.74	4	>0.05		no data	
Ss(N)	14.1 ^b					9.5	4 - 30	30
Dh	9.8 ^b						no data	
Sy	9.3 ^b						no data	
Tg	8.5 ^b					16.8	5 - 35	55
Ss(C)	3.7							

Species abbreviations as in Table 1.

Possession of common superscripts indicates no significant difference.

Species in bold are aerial mud-nesters

per cell was not significant (Fig. 6). Any existing correlation may therefore have been masked by other factors.

The data suggest the following alternative explanations for the different levels of parasitism observed.

Chalybion laevigatum - many prey per cell with correspondingly longer times to complete provisioning, the absence of a temporary plug during the day and no guarding of the nest may all have contributed to higher levels of parasitism. It was observed that the relatively thin cell partitions also resulted in the invasion of neighbouring cells by miltogrammine maggots, which may account for this species suffering the highest mortality due to this parasite.

Auplopus vitripennis and *A. femoralis* - significantly lower parasitism in both species may partly be due to the use of only one prey per cell. Also, extremely hard and relatively thick partitions in the former species probably reduce invasion of neighbouring cells while extensive guarding in the latter species seems to have eliminated *Miltogramminae*.

Tricarinodynerus guerini - parasitism was low in spite of prey per cell being significantly higher than in *C. laevigatum* ($t=3.47$ $df=89$ $p<0.001$). Extensive nest guarding occurs in this species, provisioning in some instances being progressive. Also, it is the only one with a nest turret at the entrance, though the effect of this on *Miltogramminae* is not known.

Sites in buildings. Similar tests were carried out on data from trap-nesters and aerial mud-nesters

from buildings (Table 14). *Chalybion laevigatum* again suffered the highest level of parasitism by Miltogramminae compared with all the other species including aerial mud-nesters.

Parasitism of the four aerial mud-nesters in Natal did not differ significantly (Table 14), a surprising result since *S. analis* provisions progressively and guards its nest extensively, the remainder mass-provisioning and leaving their nests open and unattended for considerable periods. Other unidentified factors must have been playing a role.

In general, only three species, *C. laevigatum*, *I. pelopoeiformis* and to a lesser degree *P. meadewaldoi*, were relatively heavily parasitised by Miltogramminae (Tables 12 and 14). Species common both to sites in buildings and bush sites showed the same trends, high levels of parasitism in *C. laevigatum* and low levels in *T. guerinii*, indicating a genuine difference in these species' susceptibility to Miltogramminae rather than being due to habitat effects.

CHIRYSIDIDAE

Again, there was one predominant species, *Chrysis* sp. *wahlbergi* group, which showed a wide host range but excluded the trap-nesting *Isodontia* spp. and aerial mud-nester *A. aethiopicus*. This species of *Chrysis* was apparently replaced by another of the *succincta* group in *Isodontia* nests, possibly a reflection of the vegetable cell partitions and plugs compared with the mud partitions used by other species. *Stilbum cyanurum* (Forster) was apparently confined to the single- or two-celled aerial mud-nests of *A. aethiopicus* and *D. hottentottum* respectively. The remaining species were uncommon and it is doubtful if their host selection indicated in Table 13 is comprehensive. For the analysis, it was assumed that modes of attack were similar for all the chrysidids, i.e. during provisioning.

Bush sites. Data from all samples were subjected to t-tests on the assumption that parasitism was not influenced by the sampling. *Tricarinodynerus guerinii* and *C. laevigatum* were significantly more heavily parasitised than *A. femoralis* and *A. vitripennis* (Table 15). *Isodontia pelopoeiformis* was significantly more heavily parasitised than *A. vitripennis* but did not differ from any of the other species.

As with Miltogramminae, the composition of cell partitions and end seals, cell linings, presence or absence of vestibular cells or cocoon type are unlikely to affect parasitism by Chrysididae. Nest guarding by *T. guerinii* which apparently reduced parasitism by Miltogramminae seemed not to be effective against Chrysididae. However, in this case there was a significant correlation between numbers of prey per cell and levels of attack (Table 15)(Fig. 6). Minimal opportunities for oviposition occurred in nests of *A. vitripennis* and *A. femoralis* (one prey per cell), coinciding with the lowest levels of parasitism. With the latter species, nest guarding is likely to be an important factor as well. Parasitism of *I. pelopoeiformis* in Natal did not differ significantly from that in the Cape (Table 15).

Sites in buildings. Trap-nesting species in building sites all used several prey per cell and differences in this characteristic cannot explain the significantly lower parasitism in nests of *P. meadewaldoi* and *C. laevigatum* compared with *T. guerinii*. Except for *C. laevigatum* they all guarded their nests and showed evidence of progressive-provisioning. Therefore, neither of these characteristics were effective against Chrysididae. The lower level of parasitism in *C. laevigatum* compared with *T. guerinii* is interestingly reflected in bush sites, albeit not significantly. However, the reason for the difference is not known.

Synagris analis was the only aerial mud-nester not to be affected by Chrysididae (Table 15), presumably because of progressive-provisioning and extensive nest guarding. The remaining three species showed similar levels of parasitism, but only *S. spirifex* and *D. hottentottum* were significantly less parasitised than *T. guerinii* which seemed to be particularly susceptible to chrysidid attack.

Although the trend was not significant, parasitism rates appeared to decrease as cells per nest increased in spite of the learning capabilities known for chrysidids (Rosenheim, 1987b). This could be another instance of the “selfish herd” mechanism (Wcislo, 1984) where cell is substituted for nest, but more data are required. As with *I. pelopoeiformis* in bush sites, parasitism of nests of *S. spirifex* did not differ significantly between the Cape and Natal sites.

TABLE 15. Results of t-tests on levels of parasitism due to Chrysididae.

Species	% parasitism (arcsin)	Species pair	t-tests			Prey per cell		
	t		df	p	mean	range	n	
Trap-nesters in bush sites:								
Tg	32.1 ^a	Tg/Auf	7.31	6	<0.001	16.8	5 - 35	55
Cl	19.9 ^a	Tg/Av	10.18	9	<0.001	11.8	4 - 27	34
Ip(N)	13.4 ^{ab}	Av/Ip	3.62	9	<0.01	5.1	2 - 14	13
Auf	6.8 ^{bc}	Cl/Auf	2.48	7	<0.05	1.0		
Av	3.7 ^c					1.0		
Ip(C)	22.1 ^a							
Ip(N)	13.4 ^a							
Trap-nesters and aerial mud-nesters in/on buildings:								
Tg	25.6 ^a	Tg/Dh	2.50	12	<0.05			
Af	19.3 ^{ab}	Tg/Ss	2.71	7	<0.05			
Dh	16.0 ^b	Tg/Pm	2.50	12	<0.05			
Ss(N)	11.9 ^b	Tg/Cl	4.18	9	<0.01			
Pm	10.7 ^b	Af/Cl	1.55	9	>0.10			
Cl	8.0 ^b							
Sy	0.0							
Ss(C)	16.5 ^a							
Ss(N)	11.9 ^a							

Species abbreviations as in Table 1.

Possession of common superscripts signifies no significant difference.

Species in bold are aerial mud-nesters.

Chrysididae were therefore more important in aerial mud-nests, parasitising 3 of 4 species at Natal sites at relatively high levels compared with 1 or 2 of 7 trap-nesting species (Table 12). *Tricarinodrynerus guerini* was particularly susceptible both in building sites and bush sites, again indicating a true species susceptibility (Table 12).

MUTILLIDAE

Four species were recorded, one of which, *Antennotilla* sp., occurred only in trap-nests in bush sites (Table 13). The remainder were mostly confined to sites in/on buildings where populations of

hosts tend to be greater and the location of nests by the wingless females easier. *Dolichomutilla sycorax* (Smith), one of the most commonly recorded species, appeared to specialise mostly on large multi-celled aerial mud-nests, occasionally parasitising trap-nesters such as *T. guerinii* that occurred in close proximity to their main hosts. *Stenomutilla syrinx* (Peringuey) appeared to have a wider range of hosts, but again mostly in building sites.

TABLE 16. Results of t-tests on levels of parasitism due to Mutillidae and *Osprynchotus* sp.

Species	% parasitism (arcsin)	Species pair	t-tests		
			t	df	p
Mutillidae - trap-nests in bush sites:					
Auf	11.6 ^a	Auf/Cl	1.42	7	>0.10
Ip(N)	9.9 ^a				
Av	7.6 ^a				
Tg	6.1 ^a				
Cl	3.4 ^a				
Is(N)	0.0				
Ip(C)	0.0				
Mutillidae - trap-nests and aerial mud-nests in/on buildings:					
Sy	15.5 ^a	Sy/Ss(N)	1.27	4	>0.10
Af	10.9 ^a	Sy/Cl	2.51	6	<0.05
Dh	10.6 ^a	Sy/Tg	3.72	7	<0.01
Ss(N)	7.6 ^a	Ss(N)/Tg	2.84	7	<0.05
Pm	4.3 ^{ab}	Sy/Pm	0.99	9	>0.10
Cl	3.4 ^b				
Tg	1.3 ^b				
Ss(N)	7.6 ^a	Ss(N)/Ss(C)	2.31	4	>0.05
Ss(C)	0.8 ^a				
<i>Osprynchotus</i> sp. - trap-nests and aerial mud-nests in/on buildings:					
Af	19.1 ^a	Ss(N)/Dh	2.43	9	<0.05
Ss(N)	18.6 ^a	Dh/Cl	3.21	11	<0.01
Dh	11.5 ^b				
Cl	3.9 ^c				
Tg/Pm/Sy	0.0				
Ss(C)	20.9 ^a				
Ss(N)	18.6 ^a				

Species abbreviations as in Table 1.

Possession of common superscripts indicates no significant difference.

Species in bold are aerial mud-nesters.

Bush sites. Bartlett's correction (Snedecor & Cochran, 1967) was applied to small samples ($n < 50$) showing zero parasitism before using the arcsin transformation. The highest level of parasitism by Mutillidae was 6.7% in *A. femoralis*, though this did not differ significantly from that in any of the other species (Table 16). There is therefore no indication that any of the nesting characteristics listed in Table 1 for trap-nesters affected parasitism by Mutillidae. It is noteworthy, however, that *A. femoralis* was the only trap-nesting species that constructed discrete mud cells all of which were accessible without having to pass through other cells first.

Sites in buildings. Mortality due to Mutillidae was notably grouped according to nest type, aerial mud-nests suffering significantly higher levels ($\geq 2.3\%$) than trap-nests ($\leq 0.9\%$) with the exception of *P. meadewaldoi* (Tables 12 and 16). Aerial mud-nests were therefore apparently more susceptible than trap-nests to attack by Mutillidae. Thickness of daubing seemed to have no influence on levels of parasitism, suggesting that Mutillidae either are not deterred by thick nest walls or invade nests while they are still open. If the latter is the case, progressive-provisioning and nest guarding by *S. analis* was not effective against Mutillidae.

ICHNEUMONIDAE: Osprynchotus sp.

Bush sites. Attacks in bush sites were confined to nests of *C. laevigatum*, though at low levels (1.9%) (Table 12). This species did not incorporate vestibular cells into its nests and it is significant that only outer terminal cells were parasitised, a result of the observed fact that *Osprynchotus* drills through end seals with its ovipositor. Nests of *I. pelopoeiformis* and *I. stanleyi* also had no vestibular cells, but their very thick end plugs consisting of vegetable materials would deter such methods of oviposition.

Sites in buildings. All the aerial mud-nesters except *S. analis* were parasitised by *Osprynchotus* sp., *A. aethiopicus* and *S. spirifex* at levels significantly higher than *D. hottentottum* (Table 16). The exceptionally thick walls and seals of *S. analis* nests appeared to prevent oviposition. The high level of parasitism of the single-celled nests of *A. aethiopicus* was probably partly due to their thin mud walls facilitating oviposition. The thicker walls of nests of *S. spirifex* might be expected to have reduced levels of *Osprynchotus*. However, many smaller nests were without additional daubing; their multi-celled construction may also have counteracted any protection by increasing the rate of parasitisation of cells compared to that in the more widely dispersed single-cell nests of *A. aethiopicus*. The 2-celled nests of *D. hottentottum* were similarly dispersed to those of *A. aethiopicus*; however, their thicker walls may have provided some protection. It is noteworthy that only 11.5% ($n=26$) of nests attacked by *Osprynchotus* had both cells parasitised, suggesting that the cryptic design of these nests reduced such parasitism compared with that of *A. aethiopicus* through the failure of *Osprynchotus* to detect the presence of two cells.

Chalybion laevigatum was again the only trap-nester to be parasitised, albeit at a level significantly below those of the aerial mud-nesters (Table 16). Levels of parasitism of *S. spirifex* did not differ significantly between Cape and Natal sites.

ICHNEUMONIDAE: Stenarella sp.

Bush sites. Attacks by this ichneumonid were confined to nests of *C. laevigatum* and *A. vitripennis* (Table 12). A meaningful analysis of the results was not possible due to the high proportion of localities with zero parasitism (Table 8).

Sites in buildings. In contrast to *Osprynchotus*, this ichneumonid parasitised trap-nesters only

(Table 12). Again, a meaningful analysis was not possible, but none of the hosts appeared to be particularly susceptible.

Thus, the hosts of *Osprynchotus* sp. were all aerial mud-nesters with the single exception of the trap-nesting *C. laevigatum*. On the other hand, parasitism by *Stenarella* sp. was confined to trap-nesters. The range of hosts, *C. laevigatum*, *P. meadewaldoi*, *T. guerinii* and *A. vitripennis*, includes species that incorporate vestibular cells in their nests (Table 1), indicating that this nest characteristic does not prevent parasitism by *Stenarella*. Also, with *C. laevigatum*, a species that does not use vestibular cells, parasitism by *Stenarella* was not confined to the terminal cells as it was with *Osprynchotus*. Of the 15 nests affected, inner cells were parasitised in nine, outer cells in four and all cells in two of them.

Stenarella must therefore either enter nests prior to final sealing to oviposit through the most recently completed partition or directly on the cell contents of an unsealed cell, or drill through the side walls of the nest with its ovipositor. The available evidence supports the former possibility. The immunity to *Stenarella* shown by *I. pelopoeiformis* and *I. stanleyi* might appear to contradict this. However, in these species the thick cell partitions and temporary plugs of vegetable material are likely to impede oviposition and entry respectively. At the same time, this absence of parasitism strongly suggests that *Stenarella* does not oviposit through the side walls.

Contrary to expectation, guarding, as observed in *P. meadewaldoi* and *T. guerinii*, apparently did not prevent parasitisation by *Stenarella*. However, this does not necessarily support the possibility of oviposition through the side walls. The occurrence of mass-provisioning and its attendant lack of guarding in some nests of these species is the most likely explanation.

EULOPHDAE: Melittobia sp.

Due to the influence of storage on infestation levels (Table 4), analysis was confined to data from sample category 1. In buildings, *A. aethiopicus* nests suffered significantly lower parasitism than those of *S. spirifex* (Table 17). The single-celled mud pots of *A. aethiopicus* each have to be located anew by searching parasites whereas all the cells in a nest of *S. spirifex* are readily found once the nest itself has been located. The similarly low levels of parasitism in *S. analis* nests compared with *S. spirifex*, although statistically insignificant ($t=1.96$ $df=4$), suggest that particularly thick walls may reduce entry by *Melittobia*. Parasitism of trap-nesters appeared to be higher in buildings (Table 17), but none of the species that were common to bush sites and buildings differed significantly (t for *T. guerinii* =0.85 $df=6$; t for *C. laevigatum* =1.81 $df=6$).

TABLE 17. Per cent (arcsin) parasitism of cells by *Melittobia* in trap-nesting and aerial mud-nesting species.

Trap-nests (bush)		Trap-nests (buildings)		Aerial mud-nests (buildings)	
(Tg	11.4 ^a)	Tg	20.9 ^a	Ss	24.6 ^a
Auf	9.8 ^a	Cl	18.8 ^a	Dh	17.1 ^{ab}
(Ip	6.8 ^a)	Pm	13.0 ^a	Sy	8.0 ^{ab}
Av	6.2 ^a			Af	8.1 ^b
(Cl	3.4 ^a)				

Species abbreviations as in Table 1.

Species in parentheses inadequately sampled.

Possession of common superscripts within each column signifies no significant difference determined via t-tests.

All species were therefore susceptible to *Melittobia* regardless of nest type and behaviour. The data fail to demonstrate any significant differences in susceptibility except between single-celled and multi-celled aerial mud-nests i.e. nests of *A. aethiopicus* and *S. spirifex* respectively (Table 17). The possibility that *S. analis* nests are less susceptible than those of *S. spirifex* suggests that single-celled nests and thick-walled multi-celled nests may offer two alternative ways of reducing mortality from *Melittobia*, though more data are required to confirm this.

TABLE 18. Results of t-tests on parasitism of trap-nests by Leucospidae and Pompilidae: *Ceropales*.

Parasite	Host	% parasitism (arcsin)	t-tests			
			species	t	df	p
Leucospidae	Ip	26.0 ^a	Ip/Av	2.07	9	>0.05
	Av	6.7 ^a				
<i>Ceropales</i>	Auf	6.7	no t-test insufficient samples			
	Av	7.8				

Species abbreviations as in Table 1.

Possession of common superscripts indicates no significant difference.

LEUCOSPIDAE AND POMPILIDAE: *Ceropales punctulatus*

Attack by either of these parasites would not be affected by the different sample categories and thus all data were used in analysing the results (Table 18).

Leucospidae. No conclusions can be drawn with respect to the influence of nest structure or nesting behaviour on levels of parasitism. Only two species were host to Leucospidae, *I. pelopoeiformis* and *A. vitripennis*. Apart from both being trap-nesters in bush sites, they showed little in common. Type of prey, amount of provision per cell and materials used for partitions and seals differed markedly (Table 1). Since oviposition by Leucospidae is probably achieved by drilling through the side wall of the nest, the nesting characteristics considered here are unlikely to protect hosts from parasitism. Leucospidae are therefore potentially important agents in reducing nesting success in the few hosts that they select.

Ceropales punctulatus Cameron. Nests only of the pompilids *A. femoralis* and *A. vitripennis* were affected and, since oviposition occurs on the prey before it is taken into the nest, none of the nesting characteristics considered could influence levels of parasitism. Even prey cleaning would be ineffective against this type of parasite since *Ceropales* inserts its egg into one of the spider's book-lungs where it is inaccessible to the wasp. No observations were available on other aspects of behaviour during prey transportation. Specialisation on pompilid hosts means that *Ceropales* is not an important factor in nesting success of aculeate wasps in general. Insufficient data were obtained to show how important *Ceropales* may be to pompilids but levels of parasitism recorded were mostly low (Tables 9 and 12).

ENDOGENOUS MORTALITY

Bush sites. Due to the effects of opening and storage of nests, analysis was confined to data from sample categories 1 and 4 as discussed in 'Examination of the Data'. Endogenous mortality is due

to a variety of mostly unknown factors, and the reasons for any differences cannot be established from the data obtained. *Auplopus femoralis* and *A. vitripennis* suffered the highest mortality of this type amongst trap-nesters (Table 19). It is not known whether there is any significance in the fact that they are both Pompilidae.

Building sites. Endogenous mortality amongst trap-nesting species was significantly higher in *P. meadewaldoi* compared with *T. guerinii* (Table 19). Amongst aerial mud-nesters, *A. aethiopicus* suffered significantly lower endogenous mortality than *S. analis* or *D. hottentottum*. *Tricarindynerus guerinii* was the only trap-nesting species that differed significantly from aerial mud-nesters, showing lower mortality than *S. analis* or *D. hottentottum*.

Endogenous mortality accounted for significant levels of mortality in all species. Individual component factors would first need to be identified before being considered in relation to nest structure and nesting behaviour.

TABLE 19. Results of t-tests on endogenous mortality in trap-nesting and aerial mud-nesting species.

Species	% mortality	t-tests			
	(arcsin)	species pair	t	df	p
Trap-nesters in bush sites:					
Auf	26.4 ^a	Auf/Av	2.43	11	<0.05
Av	19.4 ^b	Av/Cl	2.24	9	c.0.05
Cl	12.4 ^c				
Ip	12.1 ^c				
Tg	11.5 ^c				
Trap-nesters and aerial mud-nesters in/on buildings:					
Pm	26.7 ^a	Pm/Tg	4.26	8	<0.01
Sy	22.7 ^a	Sy/Tg	2.69	7	<0.05
Dh	21.4 ^a	Dh/Tg	3.48	12	<0.01
Ss	19.4 ^{ab}				
Cl	19.4 ^{ab}				
Af	14.4 ^b				
Tg	13.4 ^b				

Species abbreviations as in Table 1.

Possession of common superscripts indicates no significant difference.

Species in bold are aerial mud-nesters.

OTHER MORTALITY FACTORS

The several other factors recorded were mostly unimportant, causing only low mortality except for sporadic higher levels at certain localities. Levels were also too low for interspecific comparison. Mean levels of attack are given in Table 20.

Bombyliidae were recorded from nests of *T. guerinii*, *P. meadewaldoi* and *A. vitripennis* and it is of interest that the presence of a turret (*T. guerinii*) did not prevent parasitism by this type of parasite. Bombyliids are known to oviposit in open holes of various kinds (Evans, 1966a; Evans & O'Neill, 1988) and to flip their eggs into nest entrances of trap-nesters while hovering in front of them (Krombein, 1967). The turret of *T. guerinii* might be expected to prevent the latter method; presumably

TABLE 20. Mortality due to various parasites and predators of minor importance averaged for all species.

Parasite/predator	Mean % mortality	Range
Bombyliidae	1.6	0.1 - 4.6
Unknown parasites	2.6	0.1 - 9.6
Mites*	2.0	0.1 - 11.5
Psocids*	4.9	0.1 - 20.5
Ants	7.7	1.3 - 45.0
	(2.4)	(1.3 - 4.5)

* - uncertain whether actually caused mortality.

a different technique for oviposition was used by the species concerned (*Anthrax pithecius* Fabricius).

Unknown parasites collectively caused similar levels of mortality.

Mortality (presumed) from mites was relatively high at only one locality (11.5%), but being associated with a small sample of only 26 cells of *C. laevigatum* from a bush site is of doubtful significance.

Psocids invaded significant proportions of cells of *P. meadewaldoi* at two building sites (11.4 and 20.5%), but these figures were based on small samples (39 and 44 cells). Only 1.1% mortality was recorded at a third site where the sample was substantial (267 cells); otherwise they occurred at similar levels to those of the other factors considered in this section. It was not definitely established whether mites and psocids had actually caused the mortality or had invaded cells after the death of their occupants.

Ants were recorded invading nests only in bush sites with one exception from a building. Mortality was low except for one site where they caused 45.0% failure of *T. guerinii* cells, again associated with a very small sample of 20 cells. However, there was evidence that ants were particularly active at this site.

It was not possible to demonstrate any species' particular susceptibility to any of these factors and therefore no links with particular nesting characteristics can be suggested.

EFFECTS OF CERTAIN CHARACTERISTICS OF AERIAL MUD-NESTS ON LEVELS OF PARASITISM

Sceliphron spirifex was the only species sufficiently well sampled to provide data on the effects on parasites of certain characteristics of multi-celled aerial mud-nests. Numbers of cells in nests (nest size), the relative positions of cells within nests and the degree of daubing have been found, or have been expected, to influence parasitism especially by *Melittobia* in other species of *Sceliphron* (Freeman & Ittyeipe, 1976; Freeman, 1982). Daubing could also be expected to reduce successful oviposition by parasites that need to drill through cell walls with their ovipositors, such as *Osprynchotus*.

Using the data from all localities, a stepwise discriminant analysis of success, with nest size, presence or absence of daubing and cell position as independent variables, showed all three variables to influence success significantly. Nest size was the most important ($F=22.258$ $df=1/1301$ $p<0.0001$) followed by daubing ($F=11.103$ $df=1/1300$ $p=0.0009$) and cell position ($F=9.165$ $df=4/1299$ $p<0.0001$). A 60.6% correct prediction of successes and failures shows that there are other unidentified factors also regulating success. The significant effects of size, daubing and cell position were

confirmed by logistic regression and loglinear analyses. The latter further indicated significant interactions between daubing and nest size (Chi-square=214.05 df=54 $p<0.0001$) and nest size and cell position (Chi-square=126.54 df=99 $p=0.0324$), but none between daubing and cell position (Chi-square=3.55 df=4 $p=0.4701$).

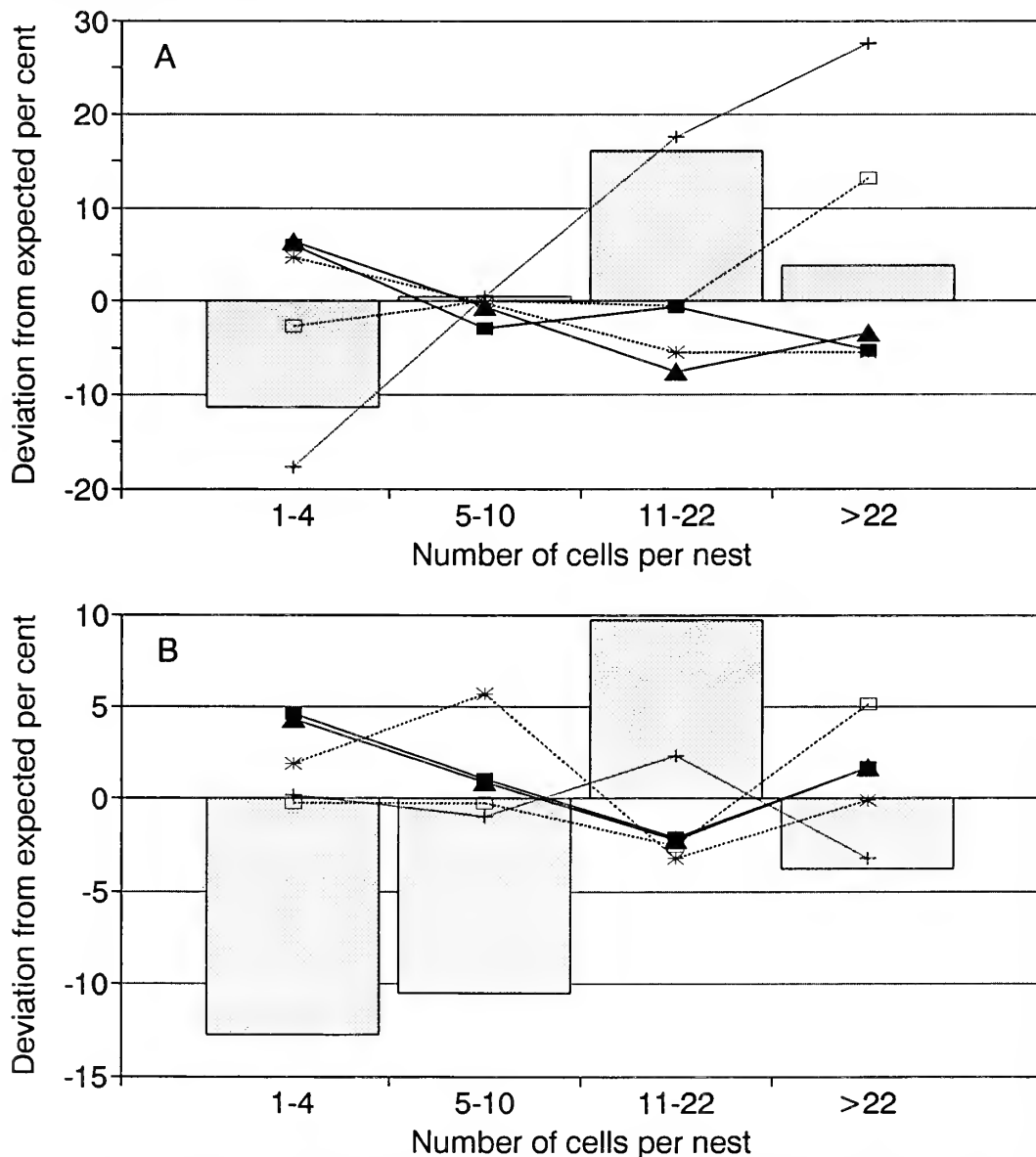


Fig. 7. Effect of nest size (cells per nest) on success rate and mortality factors in A - undaubed and B daubed nests of *Sceliphron spirifex*. + - *Melittobia*, □ - *Mutillidae*, ▲ - *Osprynchotus*, * - *Chrysididae*, ■ - endogenous mortality. Shaded bars - success rate.

TABLE 21. Effect of daubing on success rates and parasitism of nests of *Sceliphron spirifex*.

Size (cells/nest)	Daubed				Undaubed			
	1-4	5-10	11-22	>22	1-4	5-10	11-22	>22
n (nests)	36	41	39	10	39	19	5	1
n (cells)	101	298	577	288	107	170	65	24
Per cent:								
Success	10.9	13.1	33.3	19.8	14.0	25.9	41.5	29.2
Endogenous mortality	10.9	7.4	4.2	8.0	11.2	2.3	4.6	0.0
<i>Melittobia</i>	26.7	25.5	28.8	23.3	4.7	22.9	40.0	50.0
Chrysididae	8.9	12.7	3.8	6.9	10.2	5.3	0.0	0.0
Mutillidae	3.0	3.0	0.7	8.3	0.9	3.5	3.1	16.7
<i>Osprynchotus</i>	15.8	12.4	9.3	13.2	14.0	7.0	0.0	4.2
Miltogramminae	4.9	5.7	1.0	6.2	1.9	4.1	1.5	0.0

Chi-squared tests showed that success rates in both daubed and undaubed nests increased significantly with nest size except in the largest nests (>22 cells) (Table 21, Fig. 7). While undaubed nests appeared to be more successful than daubed nests, this was significant only in the 5-10 cell size category (Chi-squared = 13.83 df=1). Thus, the presence of daubing appeared to have no positive effect on overall success and, if anything, tended to result in reduced success. However, sample sizes for large undaubed nests were much smaller than those for daubed nests and additional data are required to confirm these conclusions.

Endogenous mortality decreased significantly with increasing nest size but did not differ in daubed and undaubed nests, except those in the 5-10 cell size category in which it was significantly higher in daubed nests (Chi-squared = 5.31 df=1). Endogenous mortality was therefore more dependent on nest size than on the presence or absence of daubing.

Parasitism by *Melittobia*, the most important mortality factor, depended on both nest size and daubing. Levels of parasitism were not significantly affected by size in daubed nests (Chi-squared = 2.36 df=3) but increased significantly in larger undaubed nests (Table 21, Fig. 7) (Chi-squared = 32.03 df=3). Large undaubed nests were therefore particularly susceptible to *Melittobia*, presumably due to easier penetration of the thinner walls combined with the enhanced opportunity for population increase in large nests. However, this conclusion requires confirmation with larger samples of undaubed nests, especially in the >22 cell size category. The reason for the low levels of parasitism in small undaubed nests compared with their daubed counterparts is unknown.

Parasitism by Chrysididae was significantly higher in smaller nests in both daubed and undaubed nests. Daubing appeared to result in higher chrysidid attack as well, as indicated by the significant effect in nests of 5-10 cells (Chi-squared = 6.55 df=1) though the reason for this is not known.

Daubing had no significant effect on levels of attack by Mutillidae. However, the largest nests suffered significantly higher rates of parasitism (Table 21, Fig. 7), but again this is subject to confirmation from larger samples.

Size had no significant effect on parasitism by *Osprynchotus* in daubed nests. However, there was a significant decline in parasitism with increasing size of larger undaubed nests. Therefore, contrary to expectation, daubing does not seem to deter oviposition by such parasites.

Generally, then, mortality due to the more important factors declines with increasing nest size until a certain size is reached after which this trend appears to be reversed, indicating that there is an

optimum size, probably within the 11-22 cell size category. The most important exception is *Melittobia* which increases dramatically with nest size in undaubed nests; although daubing appears to prevent this effect, it does not prevent a relatively high level of parasitism in all size classes.

Success of cells also varied according to their positions in nests (Table 22). Cells were classified according to the diagram in Fig. 3-4a. Outer cells, including those in contact with the substrate (basal outer) were significantly less successful than inner cells. Parasitism by *Ospryuchotus* was significantly higher in these cells. *Melittobia* appeared to be less prevalent in outer cells, but significance was marginal. However, there was no evidence that cells further from the substrate (outer cells) were less affected by *Melittobia* than those adjacent to it (basal inner + basal outer cells) as reported by Freeman & Ittyeipe, 1976. None of the other main mortality factors were affected by cell position. Smaller nests will tend to have an increasingly large proportion of outer cells until below a certain size the entire nest consists only of such cells. This could be one factor that helps to explain reduced success in smaller nests.

TABLE 22. Effect of cell position on success rates and parasitism of nests of *Sceliphrou spirifex*.

	Basal inner	Inner	Basal outer	Outer	Chi- square	p
n (cells)	380	226	348	465		
Per cent successful cells	30.5	29.2	20.1	20.6	13.38	<0.01
Per cent failure due to:-						
Endogenous mortality	6.8	4.9	6.9	6.4	0.99	>0.80
<i>Melittobia</i>	30.5	31.9	22.7	23.4	8.06	<0.05
<i>Ospryuchotus</i>	6.8	4.4	14.6	15.9	28.72	<0.001
Chrysididae	5.3	5.3	8.6	8.6	5.30	>0.10
Mutillidae	1.6	4.9	4.9	3.4	6.98	>0.05

DISCUSSION

Extensive and apparently random variation in nesting success in individual species is one of the most obvious findings of this study (Fig. 4). Apart from a trend at certain localities for *Syuagris analis* to achieve greater success and *Sceliphrou spirifex* the least success (Tables 6, 11 and 12), there is little support for the hypothesis that overall nesting success varies according to nesting habit. However, interlocality variation may have obscured any more subtle interspecific differences. Such variation has been reported for several species, including *Delta uaxillosum* (Chapman, 1959), *Sceliphrou laetum* (Smith, 1979), *Trypoxylon tenocitlau* (Coville & Coville, 1980), *Crabro argusinus* (Matthews *et al.*, 1979), *Tachysphex teruinitatus* (Spofford *et al.*, 1986) and *Oxybelus sericeus* (Hook & Matthews, 1980), attributable in each instance to varying levels of attack by certain nest parasites or differences in types of parasites present.

This study, as well as reports in the literature (Freeman & Parnell, 1973; Taffe & Ittyeipe, 1976; Peckham, 1977; Freeman, 1982; Spofford *et al.*, 1986; Rosenheim & Grace, 1987), show that nest parasites and predators are indeed the major cause of nest/cell failure. Mean mortality due to natural

enemies for a mixture of host species, expressed as a percentage of total mortality, calculated from 12 papers with suitable data (Appendix A), is 69.2% (range 37.8-98.8%). Figures from the current study are very similar, 62.5% (range 31.0-94.1%). It seems likely that similar sets of figures would be obtained wherever such studies are conducted. Nesting success must therefore depend largely on factors that affect levels and types of parasitism whether or not they are connected with nesting habits. They fall under three headings, "external" factors not related to nesting habits, nest structure and nesting behaviour.

External factors. These are particularly prone to variation between localities. Environmental/climatic conditions (Rau, 1916; Matthews *et al.*, 1979) prior to, during and after nesting are likely to affect nesting success, but such parameters have never been measured (Rosenheim, 1989). Characteristics of the nesting site/substrate and vegetational cover (Taffe & Ittyeipe, 1976; Freeman, 1982; Rosenheim, 1988) may also affect success rates and parasitism. However, contributions from such factors towards observed variations in parasitism and/or nesting success in this study cannot be assessed because of the lack of data. It would in any event be very difficult to separate the effects of each factor in the absence of experimental manipulation.

Parasite populations may also depend on the density and extent of the population of the host species in question (Freeman & Parnell, 1973; Matthews *et al.*, 1979; Wcislo, 1984), which is at least partly a function of the length of time that the site has been used. Populations of other species at the same site prior to and during nesting of the host species, especially if they are poorly protected (Evans, 1987), may also cause a build up of parasites and determine which species are dominant (Spofford *et al.*, 1986). Such was the case at FBG where there was a long-established, substantial population of *T. guerinii*. This species together with others that utilised trap-nests at this site, *C. laevigatum* and *P. meadewaldoi*, as well as the aerial mud-nester *S. analis*, showed consistently low success and relatively high levels of attack by *Melittobia*, Miltogramminae, Mutillidae and/or Chrysididae compared with other localities (Tables 8 and 10).

Nesting behaviour. Various features connected either with nest structure or nesting behaviour during nesting have been suggested as factors that affect nest parasitism and, therefore, nesting success. Most studies deal with ground-nesting species (40/52), only six being concerned with trap-nesters and six with aerial mud-nesters. Very few, however, are supported by quantitative data.

Behavioural features include diversionary flights by provisioning adults in response to the presence of parasites (Linsley & MacSwain, 1956; Evans & Lin, 1959; Alcock, 1974 and 1975; Matthews *et al.*, 1979; Evans *et al.*, 1980; Gwynne, 1981; Hager & Kurczewski, 1985; Evans & O'Neill, 1988; Kurczewski & Spofford, 1986; McCorquodale 1986, Spofford *et al.* 1986, Spofford & Kurczewski, 1992), nest cleaning in response to parasite presence (Simonthomas & Simomthomas, 1972; Gwynne, 1981; Sheehan, 1984; Hager & Kurczewski, 1985; Rosenheim, 1987a; Evans & O'Neill 1988, Spofford & Kurczewski 1992), prey cleaning (Linsley & MacSwain, 1956; McCorquodale, 1986; Spofford *et al.*, 1986; Spofford & Kurczewski, 1992), nest guarding (Peckham *et al.*, 1973; Peckham, 1977; Coville & Coville, 1980; Hook & Matthews, 1980; Krombein, 1979; Evans & Hook, 1982a and 1982b; Coville & Griswold, 1984; Wcislo *et al.*, 1988; Spofford & Kurczewski, 1992), progressive-provisioning (Evans, 1966b and 1977; Evans & Eberhard, 1970; Krombein, 1978; Hager & Kurczewski, 1985; Gess & Gess, 1989; Weaving, 1989), delayed provisioning (Rosenheim, 1987b) and method of transporting prey (Evans, 1962; Evans & O'Neill, 1988).

Nest guarding and progressive-provisioning were the only two of the above behavioural features for which observations were obtained in this study. In *S. analis*, the only species that consistently provisioned progressively, guarding was the outcome of the females' almost continual presence in

unsealed cells containing larvae. Nest guarding in *A. femoralis* was not associated with progressive-provisioning but with nest sharing. It is likely that these species' relatively high success rates are at least partly attributable to these behaviours.

The possible existence of alternate provisioning strategies in *T. guerinii* and *P. meadewaldoi* is of particular interest but requires further investigation, as no data were obtained to compare success rates and levels of parasitism in progressively-provisioned and mass-provisioned nests of these species. The adaptive significance of alternate provisioning strategies as displayed by *T. guerinii* and *P. meadewaldoi* has been discussed elsewhere (Weaving, 1994a). The occurrence of (slow) progressive-provisioning individuals nesting side by side with those that were (fast) mass-provisioners suggests that neither strategy is necessarily adopted by a nesting population as a whole but by individuals according to parasite pressures experienced at particular nest sites. This view is supported by the fact that individuals seemed to be able to switch from one strategy to the other (Weaving, 1994a).

Nest structure. Structural features of nests reported to affect parasitism include accessory burrows (Tsuneki, 1963; Evans, 1966a, 1966b, 1966c; Sheehan, 1984; Vinson *et al.*, 1987; Evans & O'Neill, 1988; Evans & Eberhard, 1970), burrow profile (Evans & Lin, 1959; Evans & O'Neill, 1988), nest closure (Linsley & MacSwain, 1956; Evans, 1966b; Brockmann, 1985; Hager & Kurczewski, 1985; Rosenheim, 1987a), temporary nest closure (Evans & Lin, 1959; Simonthomas & Simonthomas, 1972; Gess & Gess, 1975; Peckham, 1977; Brockmann, 1985; Spofford *et al.*, 1986; Evans & O'Neill, 1988), levelled or conspicuous tumuli (Evans & Lin, 1959; Weislo, 1984; Hager & Kurczewski, 1985; Rosenheim, 1987a; Evans & O'Neill, 1988), daubing the outer surfaces of aerial mud nests with extra mud (Freeman, 1982), building multicellular nests (Freeman & Ittyeipe, 1976; Evans, 1977), differences in nest substrates (Taffe & Ittyeipe, 1975; Freeman, 1982), numbers of cells comprising individual nests (Medler, 1964; Freeman & Ittyeipe, 1975; Evans, 1977; Freeman, 1977; Brooke, 1981; Evans & O'Neill 1988) and the inclusion of vestibular or empty cells (Evans & Eberhard, 1970; Tepedino *et al.*, 1979; Coville & Griswold, 1984; Freeman & Ittyeipe, 1993).

The species included in this study differed markedly in their overall nest structures, the thickness and materials used in construction of cell partitions and nest closures, the extent of daubing on mud nests, use of temporary closures and the inclusion of vestibular cells. However, because of the lack of significant interspecific differences in nesting success, there are no indications of links between nest structure and success except with regard to numbers of cells comprising multi-celled nests. Results indicate that there may be an optimum size at which success is maximised; for *S. spirifex* this falls within the range of 11-22 cells per nest. However, the fact that the single- and two-celled nests of *A. aethiopicus* and *D. hottentottum* respectively achieved higher levels of success suggests that the optimum number of cells in aerial mud-nests varies with species. It is also likely that such an optimum will vary even within a species according to population and types of parasites present, since the effect of nest size in *S. spirifex* differed with different parasites.

Host/parasite interactions. Significant differences in susceptibility to particular nest parasites were recorded for certain species (Tables 14-18). However, in most cases these differences cannot be definitely attributed to specific structures or behaviours because of the lack of direct observations of interactions between nesting habits and parasites. Furthermore, levels of parasitism are the outcome of the combined effects of several factors most of whose individual contributions cannot be reliably assessed from the available data.

Nevertheless, there were certain trends that should be followed up experimentally or by direct observation. Thick cell partitions of *A. vitripennis* with their very hard surfaces were associated with reduced miltogrammine parasitism; the much thinner cell partitions of *C. laevigatum* allowed invasion

of neighbouring cells by maggots which did not occur in *A. vitripennis* nests. However, this difference in susceptibility could equally well be ascribed to numbers of prey per cell. Cells of *A. vitripennis* are supplied with only one prey and are then immediately sealed, reducing the opportunity for larviposition by flies. In contrast, *C. laevigatum* cells remain open and unguarded for extended periods whilst the females hunt for the many prey required. Further observations are needed to determine which interpretation is correct. Perhaps both factors play a role.

Progressive-provisioning accompanied by nest guarding in *S. analis* is the most likely explanation for this species' lack of parasitism by Chrysididae. Yet *T. guerini*, which also employs extensive nest guarding, suffers high levels of attack. At the same time, both species similarly suffered low levels of parasitism by Miltogramminae which could also be attributed to nest guarding. Detailed observations of how such parasitism is achieved are required to explain these apparent anomalies.

Osprynchotus parasitised cells by ovipositing through the end seals of trap-nests or mud walls of aerial mud-nests. It was obvious in the case of trap-nests, as with nests of *C. laevigatum* in which parasitism was confined to terminal cells, that mortality from such parasites was due to the absence of vestibular cells. It also seems likely that very thick walls in aerial mud-nests prevent such parasitism, as demonstrated by nests of *S. analis* compared with the progressively thinner-walled nests of *S. spirifex*, *D. hottentottum* and *A. aethiopicus* (Table 16). A different pattern of parasitism by the apparently very similar *Stenarella* emphasises the importance of making observations on modes of attack. None were obtained for this species during this study, but this ichneumonid clearly uses a different strategy from that of *Osprynchotus*.

While natural enemies are considered to have controlled the development of many aspects of nest structure and nesting behaviour (Wcislo *et al.*, 1985; Spofford *et al.*, 1986; Rosenheim, 1987a and 1989), including the early steps leading to sociality (Rosenheim, 1989), the overall direction of evolution of nesting behaviour and nest structure is in the end determined by complex interactions between numerous factors (Wcislo *et al.*, 1985). This makes it very difficult, if not impossible, to assess the roles of individual factors, including, of course, individual types of parasites, in isolation.

A further complication that does not appear to have been considered in the literature is how representative the results obtained from a particular site are in relation to the species' overall distribution. This is of particular importance in comparative studies such as the present one. The sites used in this study represent only a minute portion of each species' incompletely known overall distribution. It is often not known whether the sites are in a marginal or more central part of each species' range, nor how nesting success varies in different parts.

In conclusion, the present results indicate that the activities of parasites are a major factor in regulating nesting success in solitary wasps. Since no species is equally protected against each type of parasite, the extensive variation in nesting success that does occur is a reflection of the size and species composition of parasite populations present at each site at the time of nesting. A high level of success will be due either to low populations of nest parasites at the locality in question, regardless of nesting behaviour, or to the fact that the species concerned is well protected, by virtue of certain nesting habits, against the dominant parasite that is present.

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Appendix A. Success rates and mortality factors extracted from published accounts.

Sp	Per cent success and parasitism							n
	SE	EM	DP	CH	MU	OS	MT	
AERIAL MUD-NESTS								
<i>Auplopus esmeralda</i> (Kimsey, 1980)	(72.5)							95(1 nest)
<i>Delta maxillosum</i> (Chapman, 1959)	(62.0)		38.0(22-51)					234
<i>Eumenes alluandi</i> (Brooke, 1981)	65.9	8.2					2.7	large
	73.0	(sealed cells)						
	5.0	(unsealed cells)						
	62.0	(c.3 cells/nest)						
	90.0	(16-26 cells/nest)						
<i>Eumenes colona</i> (Taffe & Ittyeipe, 1976)	57.7		10.3					1268
	70.0		14.1				21.1 rocks	
							0.4 roots	
<i>Pachodynerus nasidens</i> (Jayasingh, in Taffe & Ittyeipe, 1976)							27.5 substrate	
							0.0 hanging	
<i>Paraleptomenes mephitis</i> (Krombein, 1978)	(85.0)		11.5	DP+HY	1.5			181
<i>Sceliphron asiaticum</i> (Freeman, 1982)	56.2	4.3	1.5	0.1		2.6	32.6	1280
<i>S. assimile</i> (Freeman, 1977 and 1973)	61.1						28.6	17059
	59.9	8.3	0.1				30.6	2290
<i>S. fistularium</i> (Freeman, 1982)	64.4	6.6	5.4	0.3		1.5	19.7	1966
<i>S. laetum</i> (Smith, 1979)	61.8	21.0		7.9			7.9	1006
<i>Trypoxylon albitarsis</i> (Rau & Rau, 1916)	76.0	17.0					2.0	1282
TRAP-NESTERS								
<i>Ancistrocerus antilope</i> (Medler, 1964)	(39.5)							159
<i>Euodynerus foraminatus</i> (Medler, 1964)	(55.7)							260
<i>Isodontia pelopoeiformis</i> (Gess & Gess, 1982)	(75.0)	16.7	5.5					144
<i>I. stanleyi</i> (Gess & Gess, 1982)	(82.3)	11.8						17
<i>Odynerus erythrogaster</i> (Parker, 1984)	(78.0)	7.1		0.1	2.2			712

WEAVING: A COMPARISON OF NESTING SUCCESS IN SOME AFROTROPICAL ACULEATE WASPS

Appendix A. (continued)

Sp	SE	EM	DP	CH	MU	OS	MT	n
<i>Trypargilum oryzabense</i> (Coville, 1979)	(58.0)						23.0	17
<i>T. superbum</i> (Coville & Griswold, 1984)	57.1	29.0						91
<i>T. xanthandrum</i> (Coville & Griswold, 1983)	77.7	11.1		5.5				36
<i>Trypoxylon tenoetilan</i> (Coville & Coville, 1980)	56.0	7.0		36.0				144
GROUND-NESTERS								
<i>Ammophila dysmica</i> (Rosenheim, 1987a)	48.0	9.1	3.3	25.1	0.0			275
<i>A. ferrugineipes</i> (Weaving, 1989)	(93.6)		3.2					37
<i>A. insignis</i> (Weaving, 1989)	(69.3)		3.1					65
<i>A. harti</i> (Hager & Kurczewski, 1985)	(80.0-96.0)	4.0						245
<i>Bembecinus cinguliger</i> (Gess & Gess, 1975)	(97.4)							39
<i>B. oxydorcus</i> (Gess & Gess, 1975)	(100.0)							16
<i>Centris flavofasciata</i> (Vinson <i>et al.</i> , 1987)	(41.0)							22
<i>Cerceris fumipennis</i> (Evans, 1971)	(78.8)	9.6	11.5					52
<i>Crabro advena</i> Evans <i>et al.</i> , 1980)	(14.0-100)							
<i>C. cribrellifer</i> (Evans <i>et al.</i> , 1980)	(48.6)		51.4				7/26/31	3 nests
<i>C. monticola</i> (Evans <i>et al.</i> , 1980)	(90.7)	1.9	9.3					72
<i>C. argusinus</i> (Matthews <i>et al.</i> , 1979)	(83.3-100)							107
<i>C. hilaris</i> (Matthews <i>et al.</i> , 1979)	(73.3)		26.7					?
<i>C. cribrellifer</i> (Wcislo <i>et al.</i> , 1985; Wcislo, 1984)	(69.2)		30.8					<40
	(74.9)		25.1					c.155
<i>Lyroda subita</i> (Kurczewski & Peckham, 1982)	(38.4)	4.5	47.6					20
<i>Oxybelus sericeus</i> (Hook & Matthews, 1980)	(72.0)		14.5					21
	(60.3)	36.0	3.7					75
								107

Appendix A. (continued)

Sp	SE	EM	DP	CH	MU	OS	MT	n
<i>O. subulatus</i> (Peckham, 1977)	(57.1)	0.5	19.4 - 33(5-47) no males 18(4-33) + males					361
<i>Parachilus insignis</i> (Gess & Gess, 1976)	(73.0)			8.0				38
<i>Philanthus bicinctus</i> (Gwynne, 1981)	(92.5)		7.5					40
<i>P. gibbosus</i> (Evans & Lin, 1959)	(100.0)							12
<i>P. politus</i> (Evans & Lin, 1959)	(100.0)							18
<i>P. solivagus</i> (Evans & Lin, 1959)	(97.5)		2.5					40
<i>Podalonia luctuosa</i> (O'Brien & Kurczewski, 1982)	(50.0)							10
<i>P. occidentalis</i> (Evans, 1987)	(25.1)		74.9					12
<i>Tachysphex terminatus</i> (Spofford <i>et al.</i> , 1986)	(42.1- 69.4)		57.9- 30.6					76 98
<i>T. acutus</i> (Kurczewski, 1989)	(79.0)		(21.0)					14/4/1
<i>Tachytes parvus</i> (Kurczewski & Spofford, 1986)	(89.5)		10.5					19
PLANT/WOOD-BURROWERS								
<i>Dasyproctus westermanni</i> (Gess, 1980)	(39.0)	38.0						100
<i>Mimumesa mixta</i> (Rosenheim & Grace, 1987)	(41.0)			(50.0)				548

Abbreviations for column headings:-

SE - successful cells; EM - endogenous mortality; DP - miltogramminae; CH - Chrysididae; MU - Mutillidae; OS - *Osprynchotus* sp.; MT - *Melittobia*.

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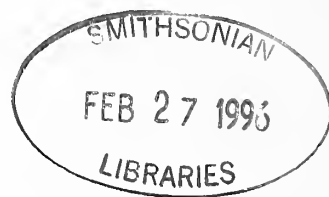
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A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian black shale near Grahamstown, South Africa

ROBERT W. GESS and NORTON HILLER



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A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian black shale near Grahamstown, South Africa

by

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ABSTRACT

A black carbonaceous shale, exposed in road cuttings that intersected rocks of the Witpoort Formation (Witteberg Group), Eastern Cape Province, South Africa has yielded a variety of fossil remains that have added considerably to our knowledge of Late Devonian life in southern Africa. The rocks are interpreted as having been deposited in a coastal setting with the black shale representing a stagnant back-barrier lagoon. Among the life forms present are charophyte and possible phaeophyte algae and a diverse array of plant types including members of the Rhyniopsida, Zosterophyllopsida, Lycopsidea and Progymnospermopsida. Arthropods are represented by the remains of Ostracoda, Conchostraca, and Eurypterida; fish by antiarch and arthrodire placoderms, acanthodians, chondrichthyans, crossopterygians and dipnoans. Several trace fossil types have also been noted.

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INTRODUCTION

The construction in 1985 of a road bypass to the immediate south of Grahamstown (Cape Province, South Africa) exposed sedimentary rocks of the Dwyka and Witteberg groups. Cuttings to the west of the junction with the Port Alfred road all contain rocks belonging to the Witpoort Formation of the Witteberg Group (Fig. 1). The Witpoort Formation is a predominantly arenaceous unit with minor interbedded shales. The new road cuttings (Fig. 2) exposed an unusually thick layer of black shale containing plant fossils. These fossils were similar to those described from a much thinner, well known shale exposed in a road cutting in Howison's Poort, about 10 km south-west of Grahamstown. However, the new material was clearly more diverse and less fragmentary.

Both algal and vascular plant material was recovered initially, including a piece of *Archaeopteris* frond.

As collecting continued, further plant material, remains of three arthropod groups and five fish groups, placoderms, acanthodians, chondrichthyans, crossopterygians, and dipnoans, were discovered.

Stratigraphic setting

The Witpoort Formation, which constitutes the middle part of the Witteberg Group, the youngest division of the tripartite Cape Supergroup, is a predominantly quartz-rich sandstone unit with minor interbedded black, grey, and maroon shales. In the Grahamstown area it is underlain by the Weltevrede Formation, consisting of shales, siltstones, and minor sandstones and overlain by shales of the Lake Mentz Subgroup.

Within the typical pale grey to white quartz arenites, quartz wackes and subarkoses of the Witpoort Formation several black carbonaceous shales up to 1 m in thickness occur at several horizons. These are often associated with fine plant fragments and trace fossils, frequently of the ichnogenus *Spirophyton*. The best known of these shale horizons is exposed at Howison's Poort. From it a few plant species have been described from fragmentary specimens (Plumstead, 1967; Anderson and Anderson, 1985; Rayner, 1988).

The relative stratigraphic positions of the shales at Howison's Poort and at the new bypass site suggest that they are probably neither continuous nor precisely contemporaneous.

Sedimentology and depositional environment

The fossil locality occurs in a road cutting approximately 500 m long and 20 m deep, where the beds dip gently (10°) northwards. The sequence has been interpreted as representing a brackish coastal back-barrier lagoon system, with significant freshwater input, sheltered by a barrier island (Hiller and Taylor, 1992; Taylor and Hiller, 1993).

The lowermost part of the sequence exposed in the cutting consists of alternating beds of brown-grey quartz arenite separated by thin shales. The quartz arenites appear largely structureless but contain

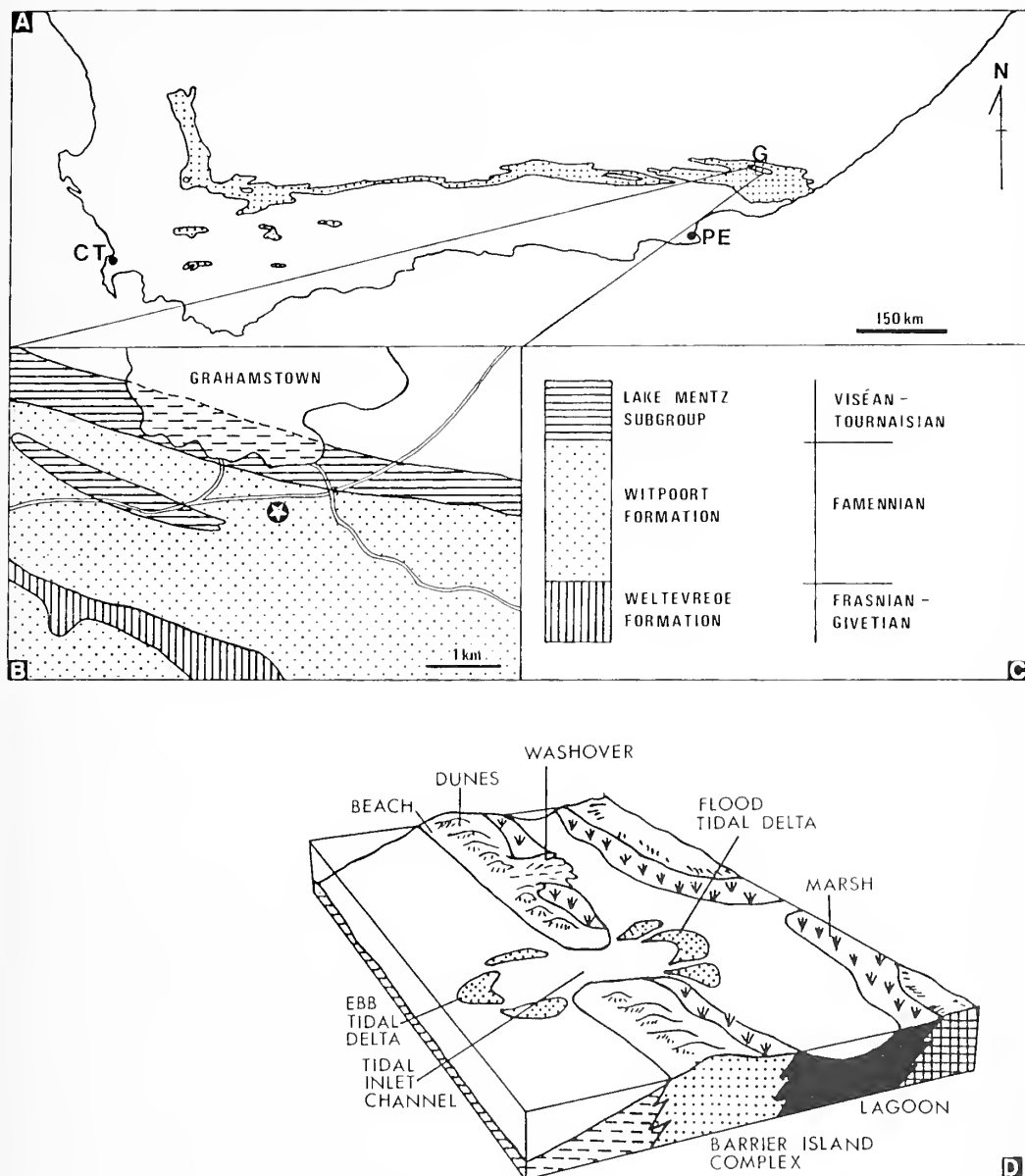


Fig. 1A-D: A. Distribution of the outcrop of Witteberg Group rocks in South Africa; B. Simplified geological map of the Grahamstown area, showing the position of the site discussed; C. Key to A and B showing correspondence with international geological time scale; D. Proposed depositional environment at the site.

some trough cross-bedding and horizontal lamination. These are overlain by about 50 m of thickly bedded, pale grey quartz arenites with occasional thin, dark grey shales and quartz wackes. Erosional contacts are common and primary structures within this sequence include horizontal lamination, ripple cross-lamination, and trough cross-bedding. This cross-bedding suggests a general westerly to south-westerly transport direction. Some bioturbation is evident in the wackes. This portion of the sequence



Fig. 2A and B: A. The road cutting from which the fossil material has been recovered; B. Gess excavating the black shale horizon.

has been interpreted as shoreface deposits passing upwards into washover, tidal channel, tidal delta, and back-barrier tidal channel deposits (Hiller and Taylor, 1992).

The middle portion of the exposed sequence, from which most of the fossil material has been recovered, consists of laminated black carbonaceous shales up to 6 m thick. These sediments represent a stagnant back-barrier lagoonal environment.

The black shales are overlain by creamy-coloured mica-rich quartz wackes containing several lenses of black shale. The top of the sequence consists of white quartz arenites displaying trough cross-bedding, ripple cross-lamination and horizontal lamination, overlain by horizontally laminated micaceous quartz wackes. This probably represents a return to a tidal delta depositional environment (Hiller and Taylor, 1992).

Age and preservation

Plumstead (1967) concluded that fossil plant fragments from the Witteberg Group were of Upper Devonian age. Anderson and Anderson (1985) agreed with this estimate at least for the Witpoort Formation. It is supported by the Early to Middle Devonian age assigned to the underlying Bokkeveld Group on the basis of marine invertebrate evidence (Boucot, Johnson and Talent, 1969). Cooper (1986), in attempting to derive a correlation with Northern Hemisphere Devonian rocks using eustatic sea-level changes, suggested that the Witpoort Formation was of Famennian age. This estimate is borne out by the presence among the material excavated during this research, of *Archaeopteris*, a characteristic Late Devonian plant, as well as *Groenlandaspis* and *Bothriolepis* placoderm fishes characteristic of this age (Young, 1989).

The fossil material from the black shale is fairly poorly preserved, taking the form of silvery white, near two-dimensional compressions. During low grade metamorphism, phyllosilicate minerals, such as mica and possibly chlorite, grew in the cavities remaining after reduction of the organic matter. These minerals subsequently altered to kaolinite during uplift to present levels. The condition of the fossils has precluded excavation in the round and digestion of material from the rock. It is also not possible to study fine details with the scanning electron microscope or high powered optical microscope.

Much of the organic remains appear to have been in a state of decay at the time of burial and the skeletal elements of the fish are partially, or completely dissociated. Water current activity in the area of greatest concentration is likely to have been very slight, suggesting that dissociation was aided by the gases of decay and the activities of scavengers.

Occurrence of the fossil remains

The majority of the fossils described in this catalogue were recovered from the carbonaceous lagoonal black shale though several robust plant structures and trace fossils were discovered in the sandstones of barrier origin that stratigraphically underlie the shale.

FOSSILS ASSOCIATED WITH THE SANDSTONES

A variety of trace fossils was discovered as sole marks on the underside of sandstone layers interbedded with thin reddish shales. The lower surfaces of the sandstones were prepared by exposing them to the elements for a few months. By far the most common types present belong to the ichnogenera *Rusophycos* and *Cruziana*, the former often associated with the end of several centimetre-long wavy

Cruziana tracks that are generally about 5 mm wide (Fig. 3A). Another interesting trace is a presumably endogenic helical structure (Fig. 3B) that may have been produced by an annelid.

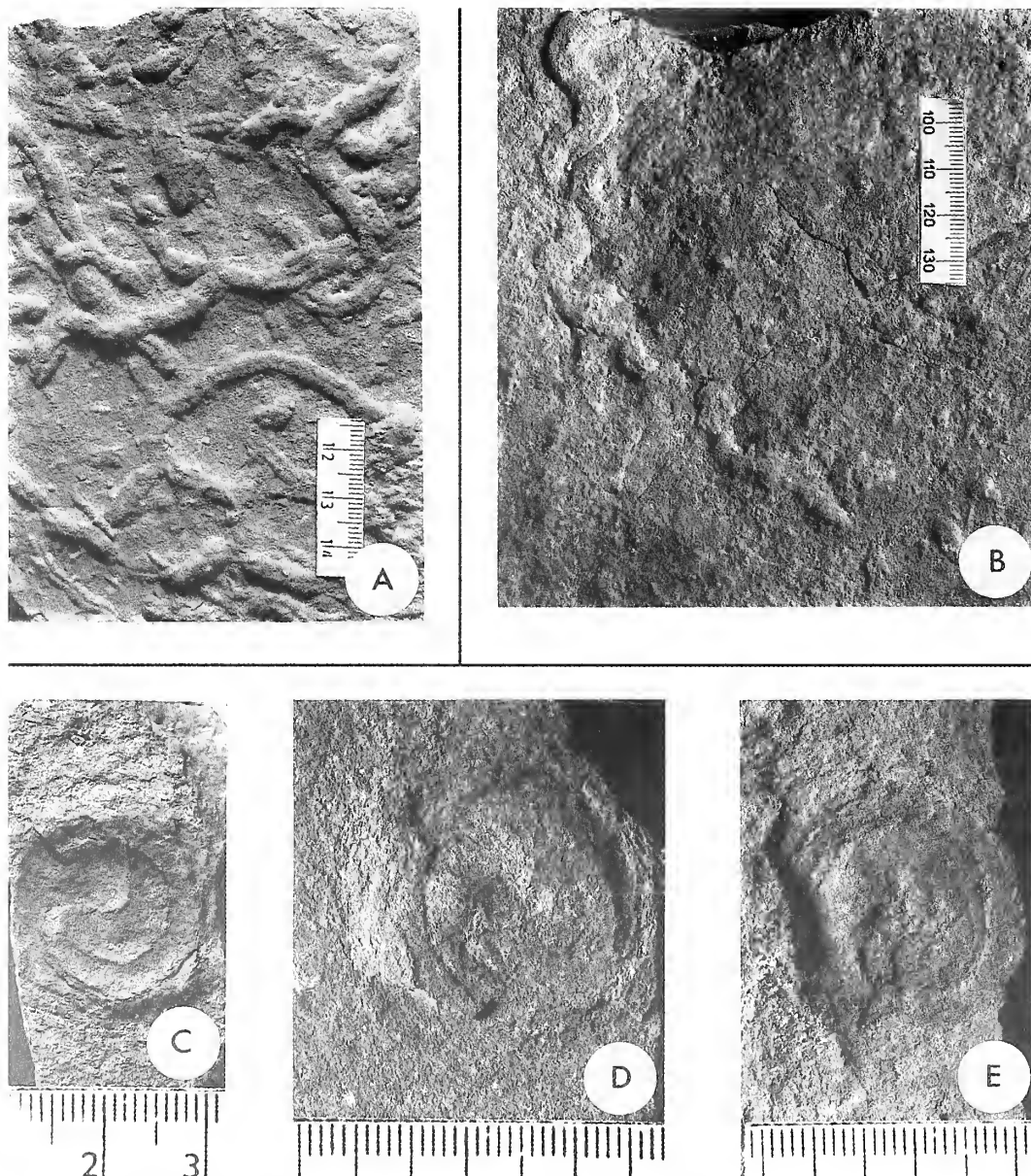


Fig. 3A-E: A. *Rusophycos* and *Cruziana* from sandstone interbedded with reddish shale; B. Helical, presumed endogenic trace from sandstone interbedded with reddish shale; C-E. "*Spirophyton*" from near the top of the black shale.

Rusophycos and *Cruziana* are generally taken to represent the resting and feeding traces respectively of arthropods, often trilobites, and to indicate a shallow marine environment. This accords with our interpretation of the area as being close to the lagoon mouth.

Within the same set of interbedded sandstones an internal cast of the stem of the lycopod *Leptophloeum* was found. This was probably washed down into the lagoon where it became stranded on the sand flats along with smaller fragments of plants that are better preserved in the black shale. Further *Leptophloeum* material, including young stems and root bases, was recovered from a mud-chip conglomerate lens where it occurred with *Haplostigma irregularis* remains (Figs 22A, D; 23A-C; 24; 27B-E).

A thin (50 mm) black shale interbedded with the sandstones has yielded several relatively well-preserved pieces of the fronds of the progymnosperm *Archaeopteris* (Figs 31, 32B). This occurrence lies below the main black shale, which yielded other *Archaeopteris* material.

FOSSILS ASSOCIATED WITH THE BLACK SHALE

Trace fossils resembling small examples of the ichnogenus *Spirophyton* occur near the top of the black shale. The specimens (Fig. 3C-E) are circular in plan view with an average diameter of 25 mm and a central shaft 6 mm across. If our identification is correct then this may represent an opportunistic occurrence in an oxygen-depleted environment (Bromley, 1990).

Plant and algal remains of both terrestrial and aquatic origin are by far the most common fossils recovered from the site. Below we document the diversity of plant types represented in the collection and offer provisional identifications where possible.

ALGAE

Phaeophyta (Figs 4-6)

A large amount of the material recovered can probably be assigned to the brown algae. The most distinctive and among the most common were provisionally reported as "terminally-lobed algae" (Taylor and Hiller, 1993), and are the subject of a separate paper (Hiller and Gess, in press).

The structure of this form is extremely variable. Typical specimens consist of thallae (or pieces thereof) with an average length of about 60 mm, but reaching up to about 120 mm in more elongate individuals (Fig. 5B). These thallae are on average 3-4 mm wide with bifurcations at irregular intervals, typically about 15 mm apart (but sometimes at negligible intervals or far greater ones). Up to seven bifurcations occur in some specimens. Micro-environmental influences such as water depth probably account for this variability. Some specimens suggest a four-lobed overall structure, perhaps arising from two very closely spaced initial bifurcations (Fig. 4A). In less than one-third of the specimens, small, round, bud-like structures occur along the edges of thalloid strands (Figs 4D-E; 5A). These may be reproductive. Two atypical specimens are also illustrated (Figs 5D; 6A). The first of these, (Fig. 5D) undoubtedly represents the development of an adventitious branch.

The specimens strikingly resemble the more fragmentary remains described as *Buthotrephis trichotoma* Douglas and Jell (1985) from the Early Devonian of central Victoria (Australia) and may represent the same form. Individuals with a negligible distance between two main bifurcations (Fig. 5C) can resemble *Hungerfordia dichotoma* Fry and Banks (1955), described from a single specimen from the Upper Devonian of New York State. We believe that the American and Australian material is of the same species. These specimens also bear a strong resemblance to the modern brown algal genus *Dictyota*.

Other more elongated dichotomously branching structures from the locality similarly lack a central strand. One specimen (Fig. 6B) calls to mind *Yeaia flexuosa* Douglas (1983) from the

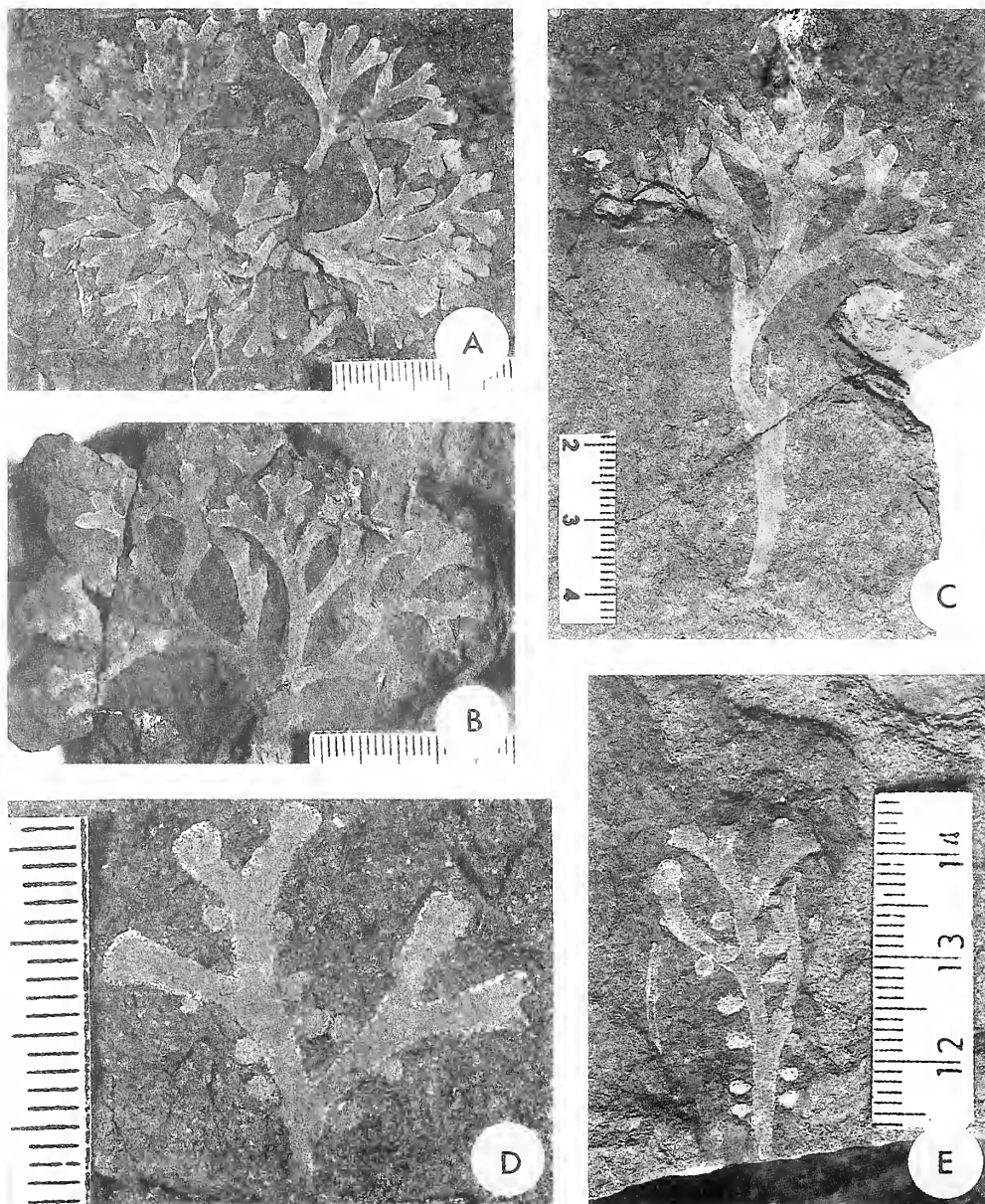


Fig. 4 A-E. *Hungerfordia*: A. Showing possible four-lobed structure; B-C. Showing well preserved dichotomising; D-E. Showing bud-like structures.

Baragwanathia flora of central Victoria. Our specimen consists of a strap-like thallus about 8-9 mm wide, showing two bifurcations 50 mm apart. The exterior is irregularly covered in dots that are presumed to be reproductive structures. Other, less complete pieces of similar but narrower straps have also been found (Fig. 6C).

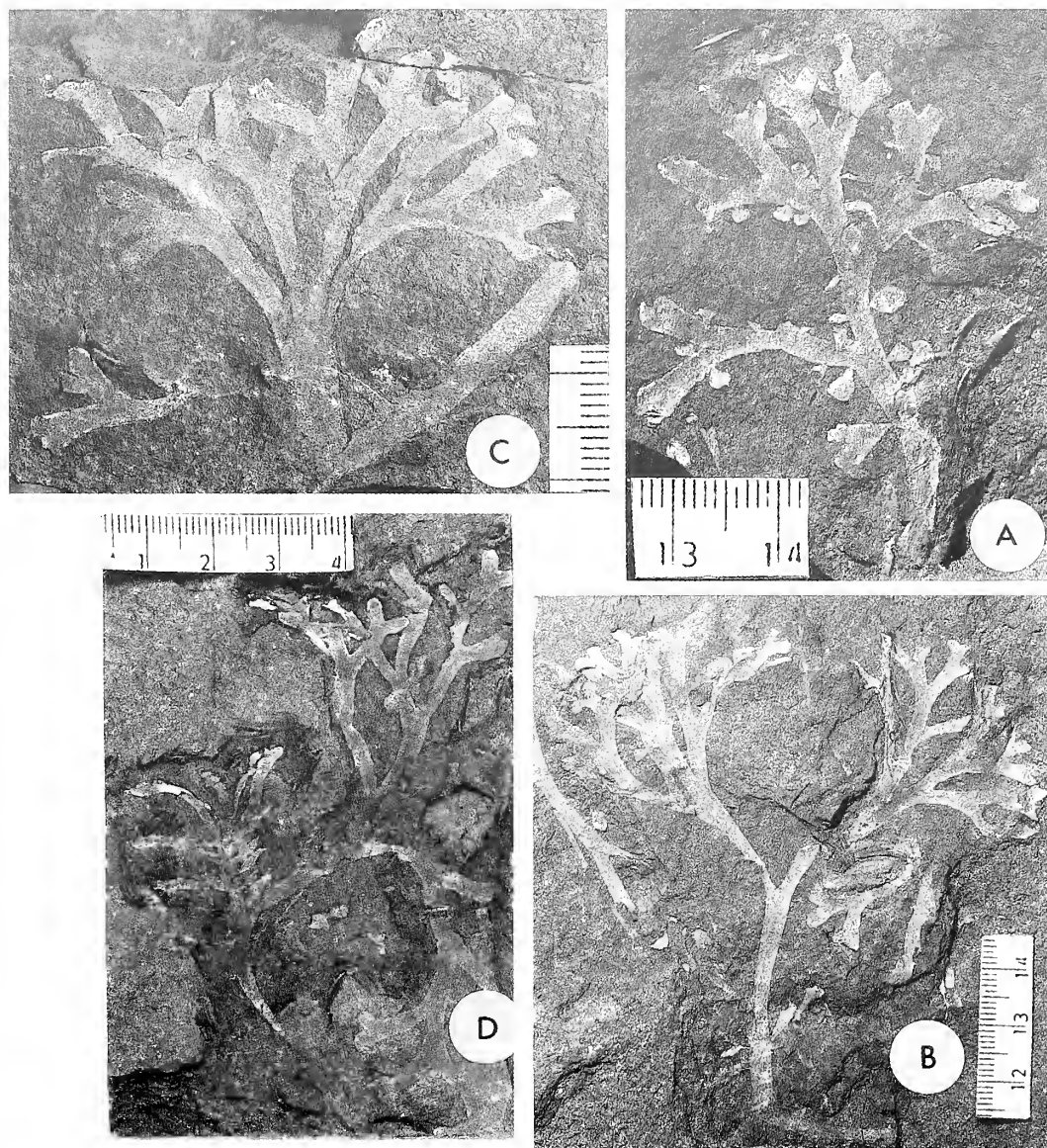


Fig. 5 A-D. *Hungerfordia*: A. Showing unusual lobes; B. Large specimen; C. Resembling type specimen of *Hungerfordia dichotoma* Fry and Banks; D. With adventitious branch.

We believe that other algal material may be represented among the *incertae sedis* (Figs 39-41).

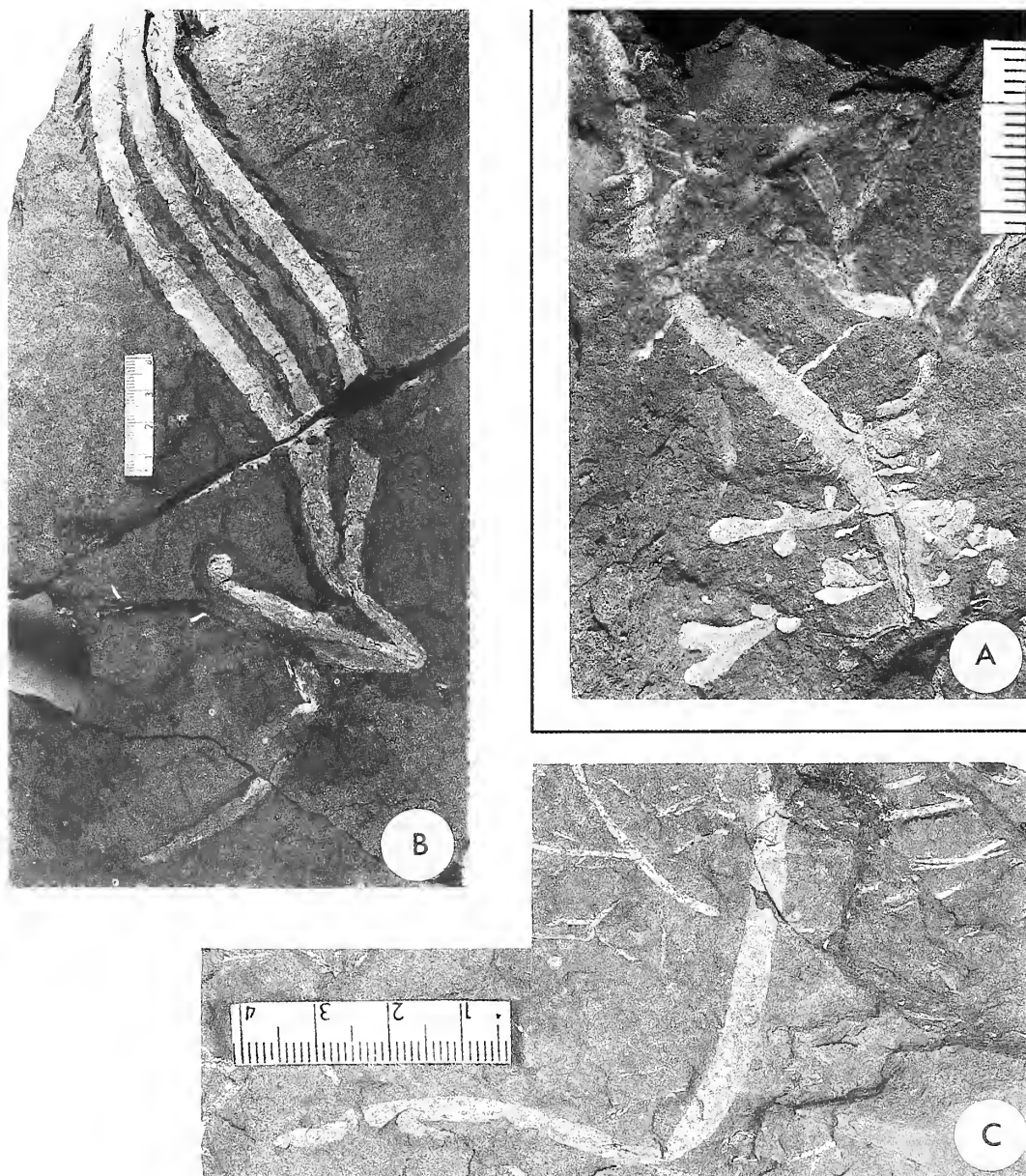


Fig. 6A-C: A. *Hungerfordia*, unusual specimen; B-C. *Yeaia* sp.

Charophyta (Figs 7-11)

During the initial investigation only a few incomplete whorls of what the authors now interpret as charophytes came to light. Their affinities were not recognised, so they were reported as “daisy-wheels” (Taylor and Hiller, 1993). However, many more isolated whorls, as well as short axes bearing whorls at the nodes, have now been found. Fossil charophytes are known largely from their reproductive structures (Hill and El-Khayal, 1983), so the discovery of associated vegetative structures afforded us a rare opportunity to suggest reconstructions for these species (Gess and Hiller, in press).

Among the forms that we confidently assign to the charophytes we recognise four species, all represented by both vegetative and reproductive structures. Two of these possess an octaradial symmetry and the other two hexaradial symmetry, and on this basis we have assigned them to two genera (Gess and Hiller, in press). The inclusion of these species in the Eocharaceae is suggested not only by their age but also by their sinistrally spiral oogonia. Direct comparison with *Eochara*, which is only known from three-dimensionally preserved isolated oogonia, is precluded because the two-dimensional preservation of our specimens does not permit examination of the crown cell and determination of the number of spiral cells (their high number being the diagnostic character of the family). All four species consist of internodes with regularly arranged fertile nodes.

The larger octaradial form (new genus 1, new species 1), with whorls of up to 14 mm in diameter, has branches that are relatively broad with rounded terminations (Figs. 8A; 9B; 10A). Each nodal whorl bears eight radially arranged branches that quadrifurcate after about one-third of their length. Oogonia, which are attached within the junction of these four sub-branches, are almost spherical, about 1.7 mm long and 1.6 mm wide at widest but tapering towards the attachment. On the upper surface of each radial branch, just before the point of quadrification, a paired oval structure may represent the antheridium (Fig. 9B).

The other octaradial form (new genus 1, new species 2), has a similar general arrangement, but with branches that are narrow with slender tapering terminations, and whorls up to 10 mm in diameter (Figs 7A-E; 9A; 10B). Oogonia of this species are ellipsoidal, about 1.5 mm long and 0.9 mm wide at widest. In one specimen the sub-branches are seen to divide again (Fig. 7E). The internodes appear uncorticated (Fig. 7A).

The internodes of the hexaradial forms (new genus 2) also appear uncorticated (Figs 8C; 8E; 11A-E). Nodes in one species (new genus 2, new species 1) bear whorls about 6 mm in diameter, consisting of six radial branches. Each branch consists of a short stalk that gives rise to a slender pointed branchlet and carries an oogonium (Figs 8B-E; 9C; 10C). Oogonia are apparently attached to the underside of branches, at the position from which the branchlet arises. The oogonia are pear shaped, about 1.6 mm long and 1.2 mm wide at the widest, tapering towards the attachment.

The structure of the other species in this genus (new genus 2, new species 2) is less well known. It has whorls of about 8.5 mm in diameter that consist of six branches. At about half their radius these branches redivide, each giving rise to a smaller whorl, bearing six relatively small oogonia, couched between branchlets arising from a further division (Fig. 11).

Although differing in superficial appearance, the architectures of these species are reminiscent of the modern genus *Nitella*.

We believe that these four charophyte species probably lived in the shallow, still, brackish water near the edge of the lagoon, close to their place of burial. Transport over any great distance would probably have led to greater damage to, or destruction of, the vegetative material.

Fragmentary remains have been discovered, suggesting the presence of a fifth species of charophyte.

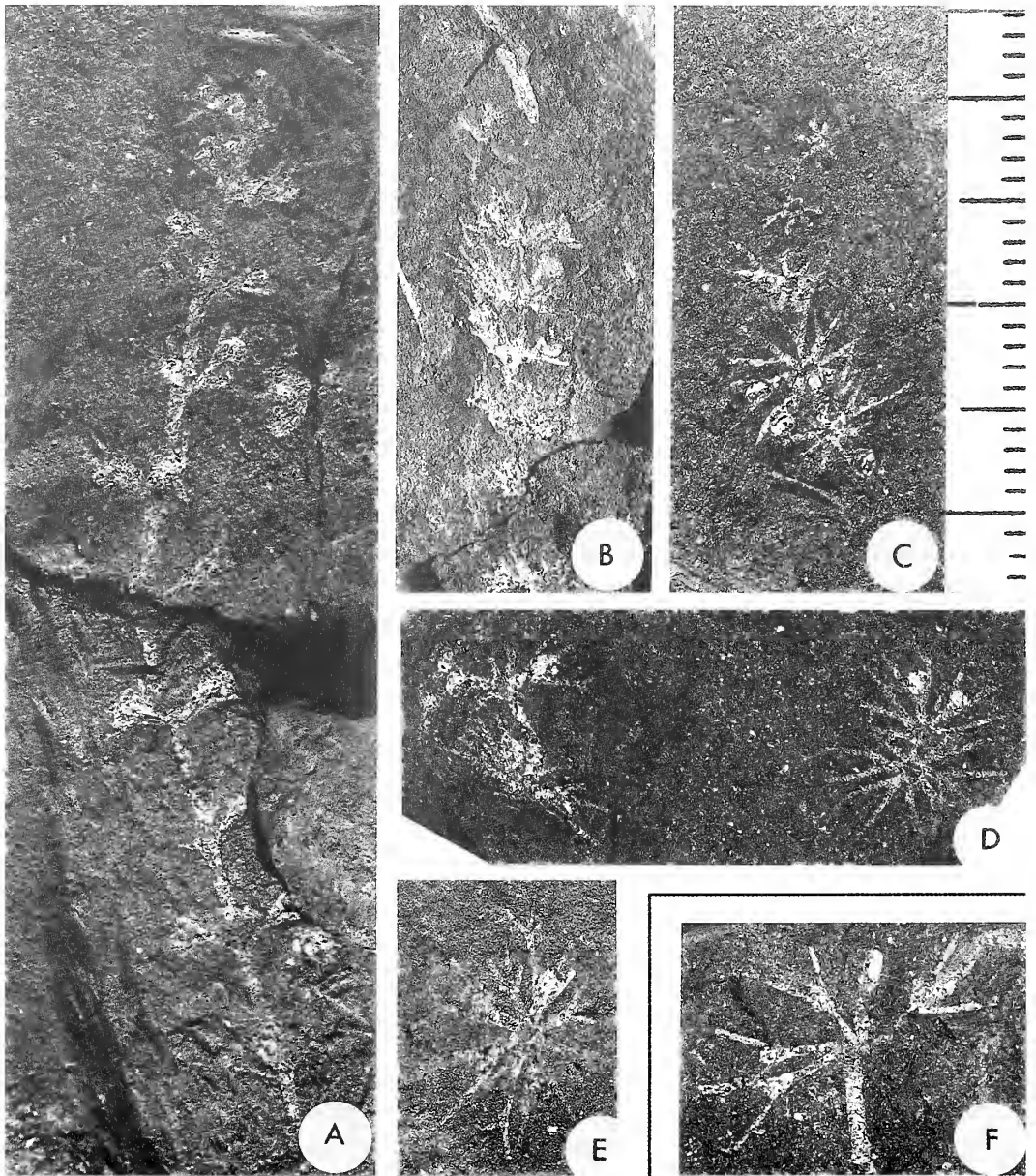


Fig. 7A-E. Charophyta, new genus 1, new species 2: A-B. Whorls on axis; C-D. Associated whorls; E. Showing sub-branches redividing; F. Possibly related specimen.

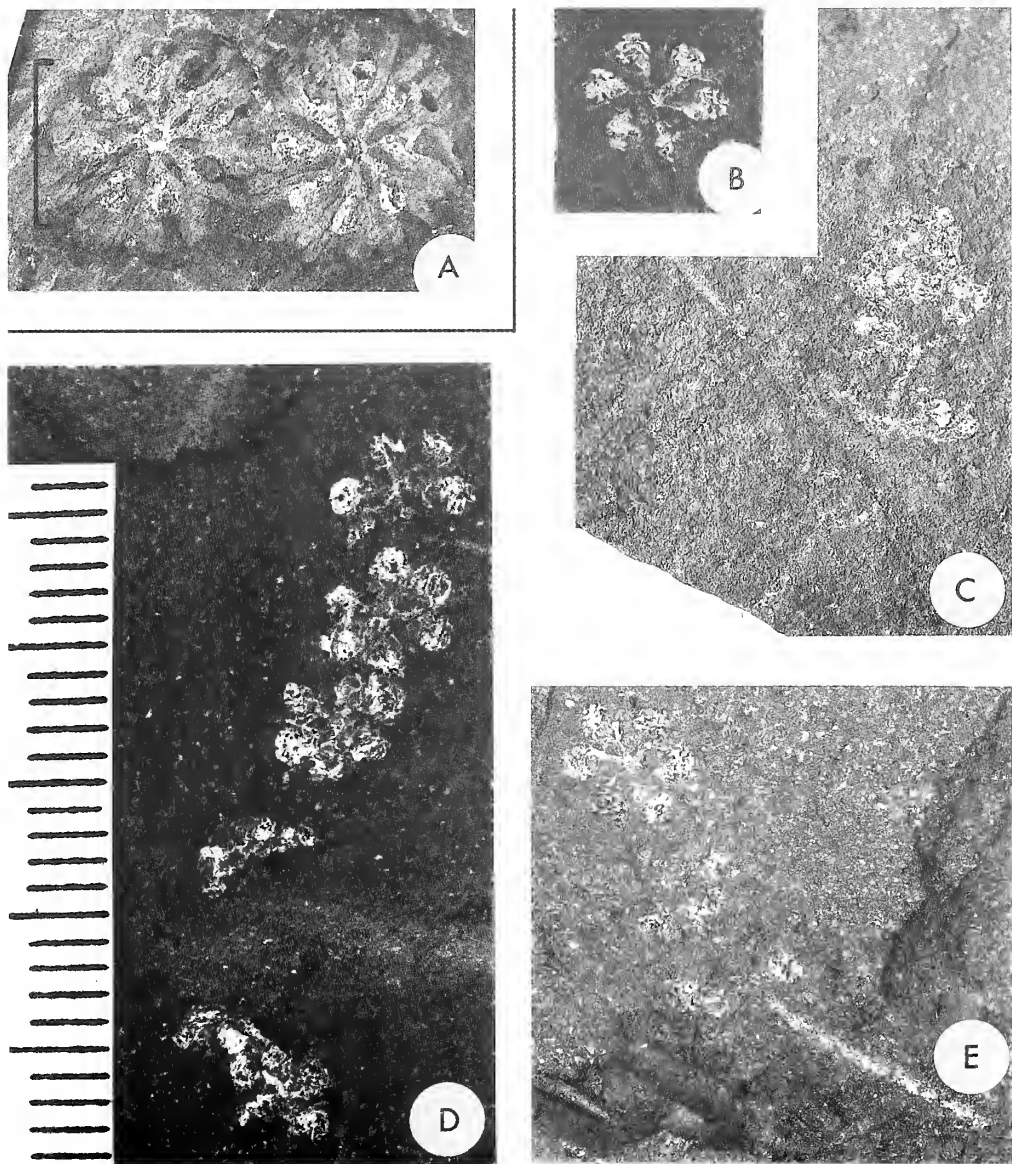


Fig. 8A-E: A. Charophyta, new genus 1, new species 1., two whorls (scale bar = 10 mm); B-E. Charophyta, new genus 2, new species 1: B. Isolated whorl; C. Growing tip; D. Chain of associated whorls; E. Whorls on axis.

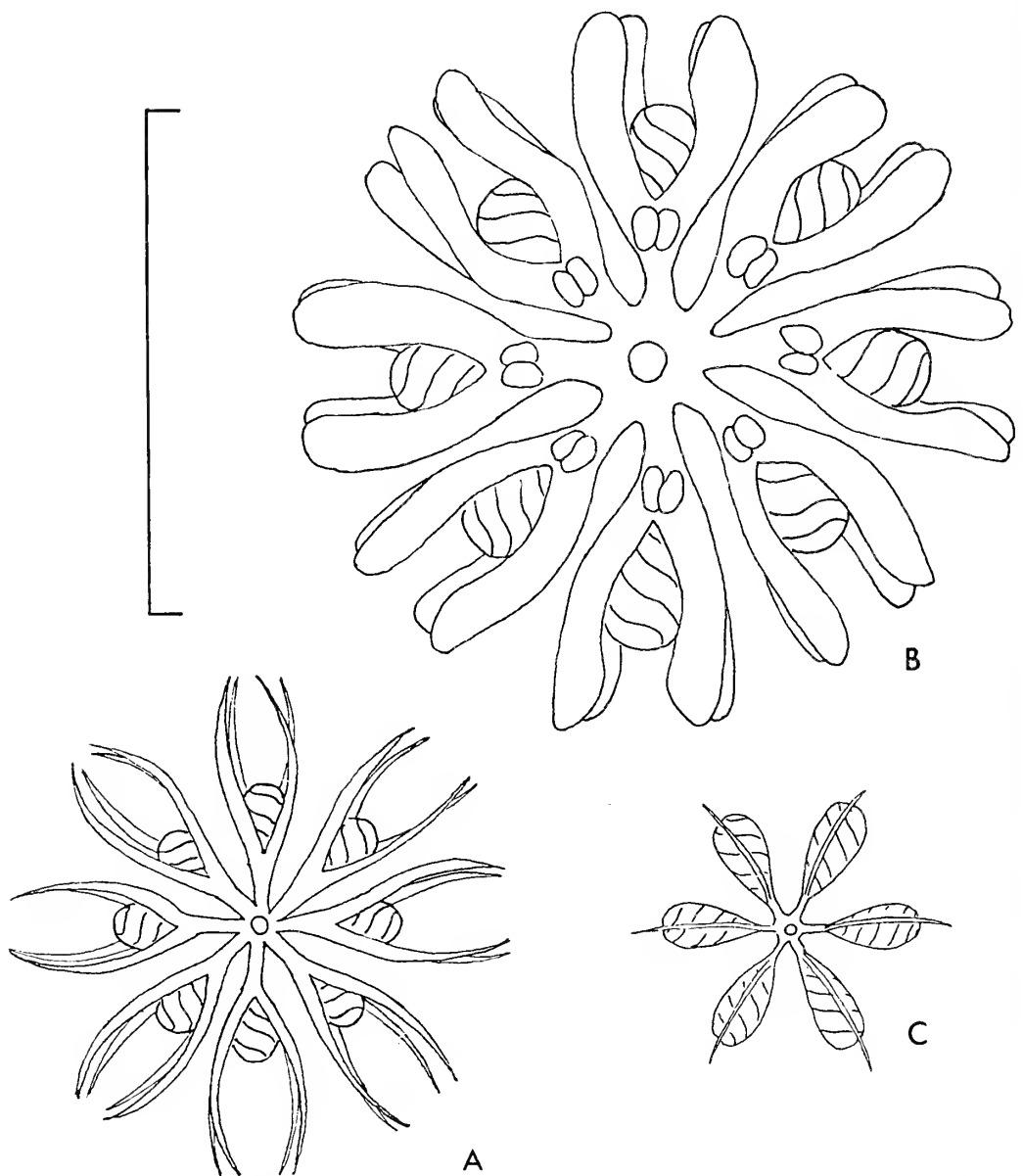


Fig. 9 A-C. Charophyte nodal whorls: A. New genus 1, new species 2; B. New genus 1, new species 1; C. New genus 2, new species 1. (Scale bar = 10 mm)

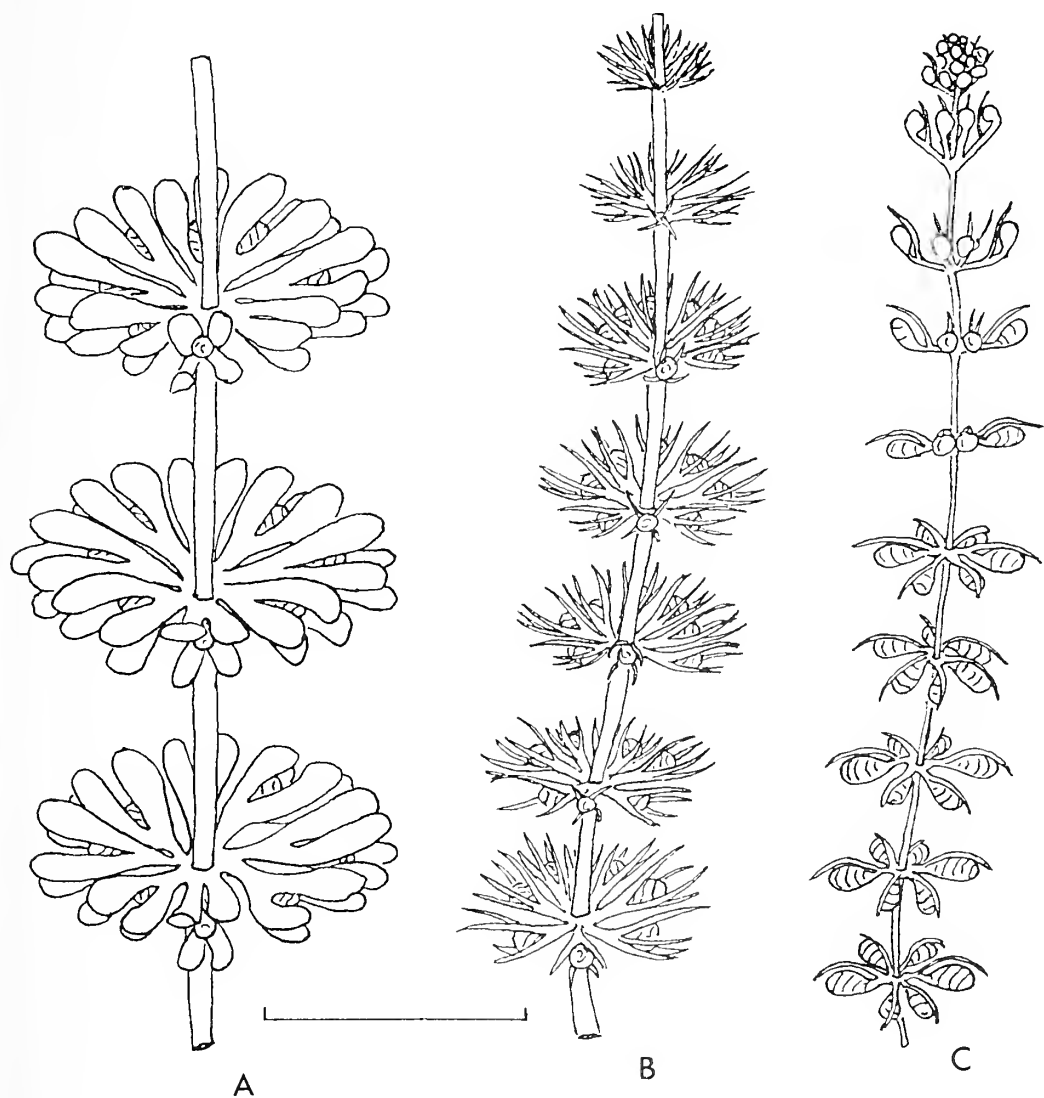


Fig. 10 A-C. Charophyte axial reconstructions: A. New genus 1, new species 1; B. New genus 1, new species 2; C. New genus 2, new species 1. (Scale bar = 10 mm)

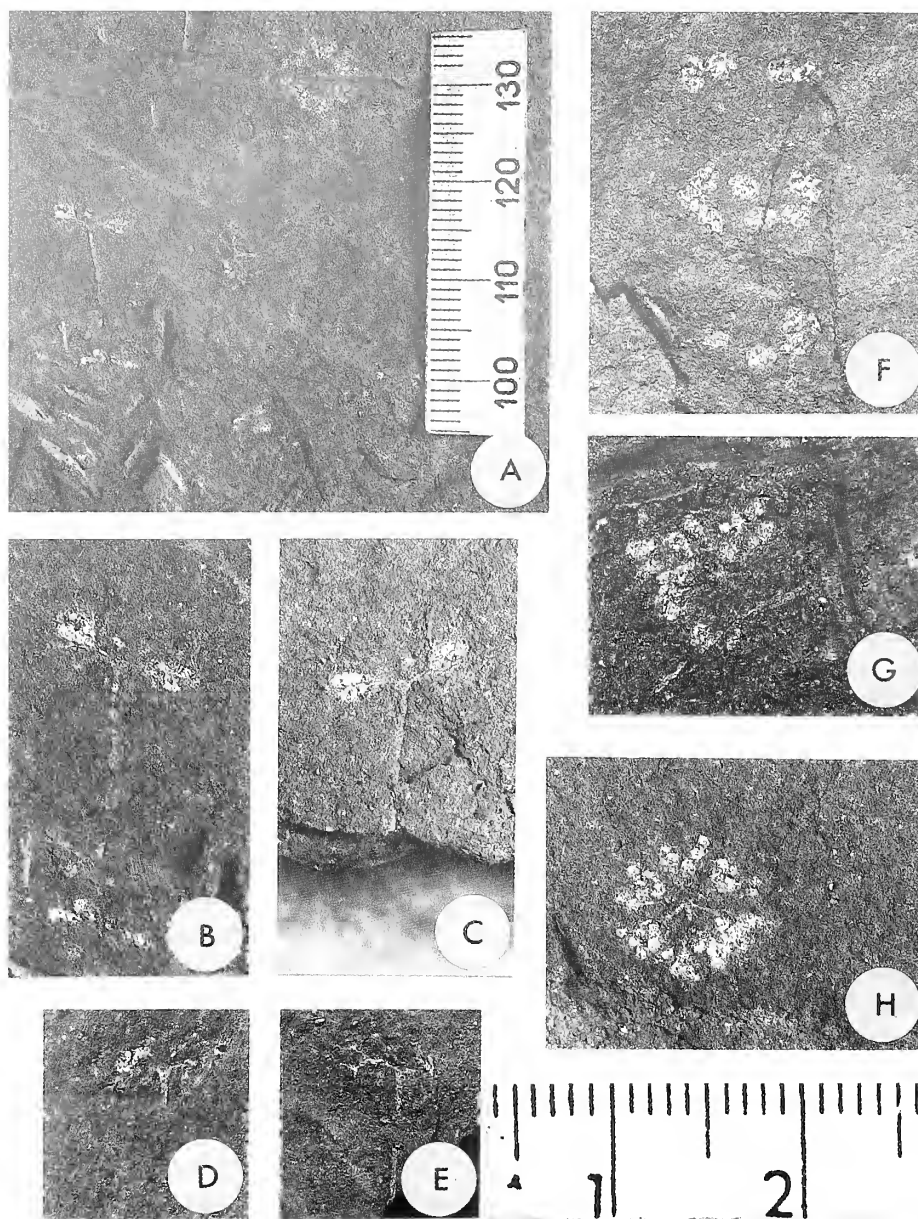


Fig. 11 A-H. Charophyta, new genus 2, new species 2: A. Specimen showing 4 whorls; B-C. Side view of whorl in A attached to axis and containing oogonia; D-E. Side view of whorl in A attached to axis and lacking most oogonia; F. Oogonia from three associated whorls; G. Oogonia attached to whorl in plan view; H. Plan view of whorl in A (counter specimen).

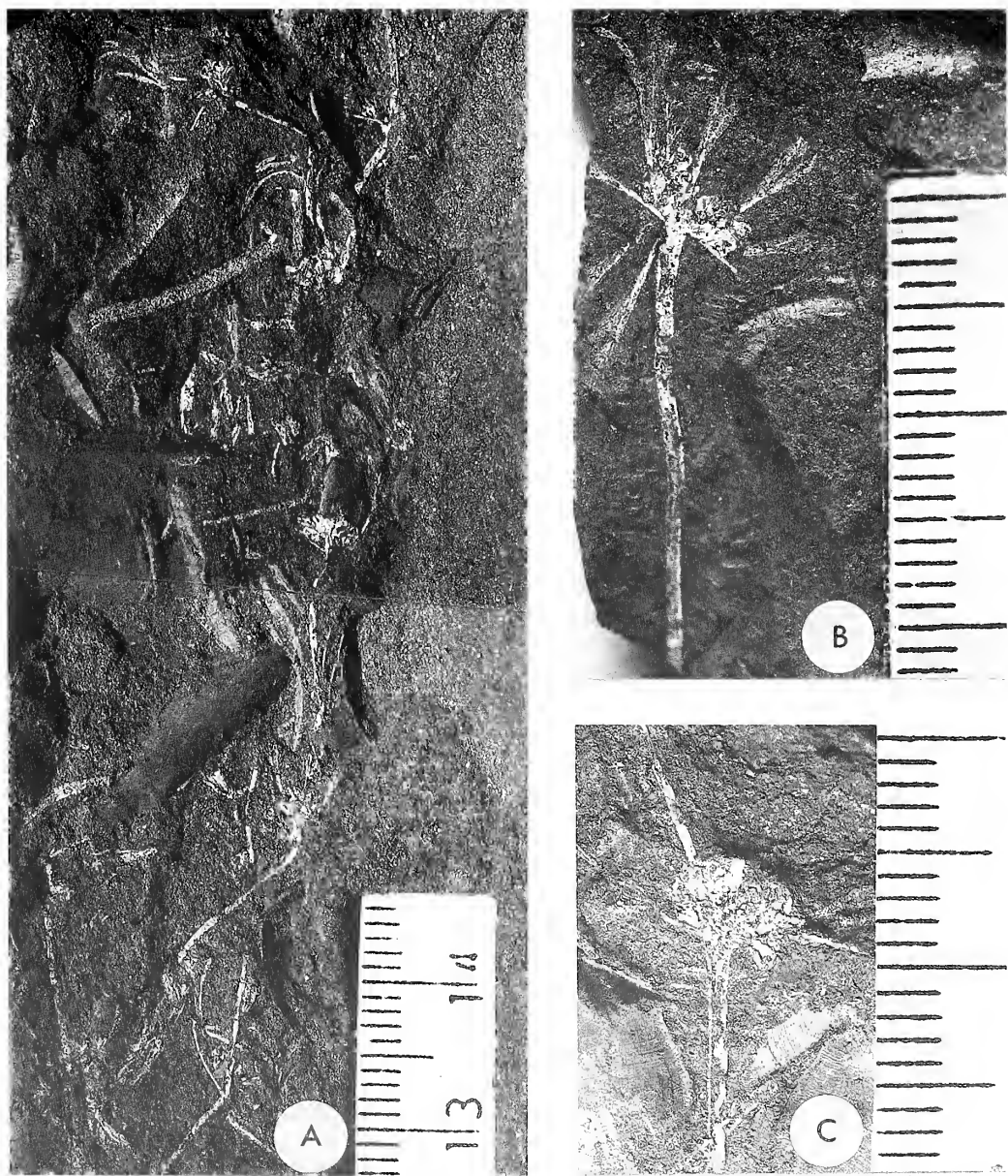


Fig. 12A-C. Presumed aquatic plant: A. Branching axes bearing leaflets and fertile nodes; B. Fertile node with well preserved bracts; C. Fertile node.

Another vegetative form bearing a superficial resemblance to the Charophyta cannot be unequivocally assigned to any group at this time, but seemingly also consists of internodes and fertile nodes (Fig. 12). Nodes occur at intervals of about 15 to 25 mm, with the fertile region having a diameter of 5 mm, and the nodal bracts circumscribing a diameter of about 15 mm. The internodes are branched and sometimes bear fine elongate "leaflets" about 5 mm long. This form is also assumed to have been aquatic.

Nodes and internodes are also observed in another presumed aquatic form (Fig. 40A-B).

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cf. Rhyniopsida (Figs 13, 14, 15A)

A single specimen has been found that the authors believe to be a gametophyte of this group (Fig. 15A) as defined by Stewart and Rothwell (1993). It has a smooth axis 48 mm long, terminating at one end in a thin putative sub-aerial axis, of which the proximal 16 mm is preserved. The other end flares into a cup 16 mm wide at the lip. This specimen bears a striking resemblance to the gametophyte genus *Lyonophyton*, though seemingly with fewer lobes around the lip of the cup.

We note that the South African species *Dutoitia pulchra* Hoeg (1930) is very similar to the genus of rhyniopsid gametophyte, *Sciadophyton*. The only significant difference between these two genera is the existence of small enations on the axis of *Dutoitia pulchra*. The authors believe the new specimen described here represents a separate species of *Dutoitia*, a genus that should be restricted for South African gametophyte rhyniopsids. The other two species added to this genus by Plumstead (1967) are apparently sporophyte material of unrelated types and should therefore be removed from *Dutoitia*.

Note that Schweitzer (1981) proposed that *Sciadophyton* is the gametophyte correlate of sporophytes of the *Zosterophyllum* and *Taeniocrada* types. *Zosterophyllum* from the Grahamstown site is discussed below.

Also present at the site are numerous specimens referable to *Dutoitia alfreda* Plumstead (1967) (Fig. 13). These plants consist of slender, dichotomously branched naked axes about 0.5 mm wide, terminating in club-shaped sporangia up to 7 mm long and 1 mm wide. As pointed out above, we believe that Plumstead (1967) was wrong to assign this species to the genus *Dutoitia* and suggest the creation of a new genus.

Closely associated on the same bedding planes with the "*D.*" *alfreda* material are other, possibly related, specimens with round sporangia 2 mm in diameter (Fig. 14). The sporangia are found attached to masses of dichotomously branched naked axes that vary from 1 mm wide at the thickest to less than 0.25 mm. The thicker axes bear sporangia on short lateral branches (Fig. 14C) whereas the thinner distal axes are often seen to terminate in sporangia (Fig. 14D).

Zosterophylloids (Figs 15B-D, 16-18)

A wealth of vegetative material attributable to the genus *Zosterophyllum* has been collected at the site, although only one fertile spike is known. It is 23 mm long with closely packed sporangia along the distal 13 mm (Fig. 15B). Unfortunately the state of preservation precludes detailed examination of the fine structures of this spike. Far more frequently found are fragmentary "leaves" and rhizomes, some showing the unusual branching forms that typify this genus (Figs 15C-D; 16A). The "leaves" reach up to 110 mm in length, and fork towards the end in typical zosterophyll fashion (Fig. 17, especially 17C). Frequently associated with these axes are spheroid structures up to 15 mm

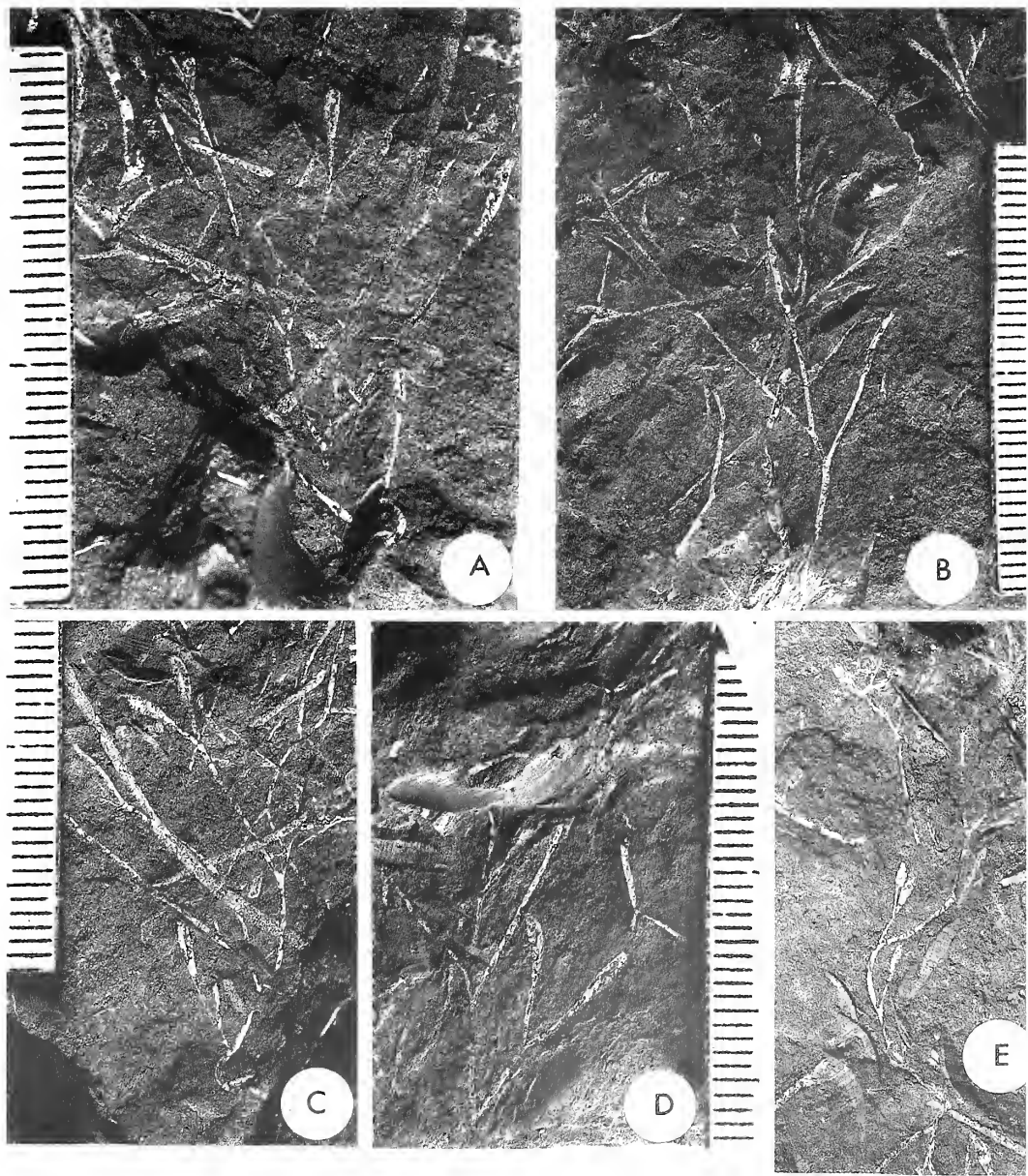


Fig. 13. *Dutoitia alfreda* Plumstead, a possible rhyniopsid.

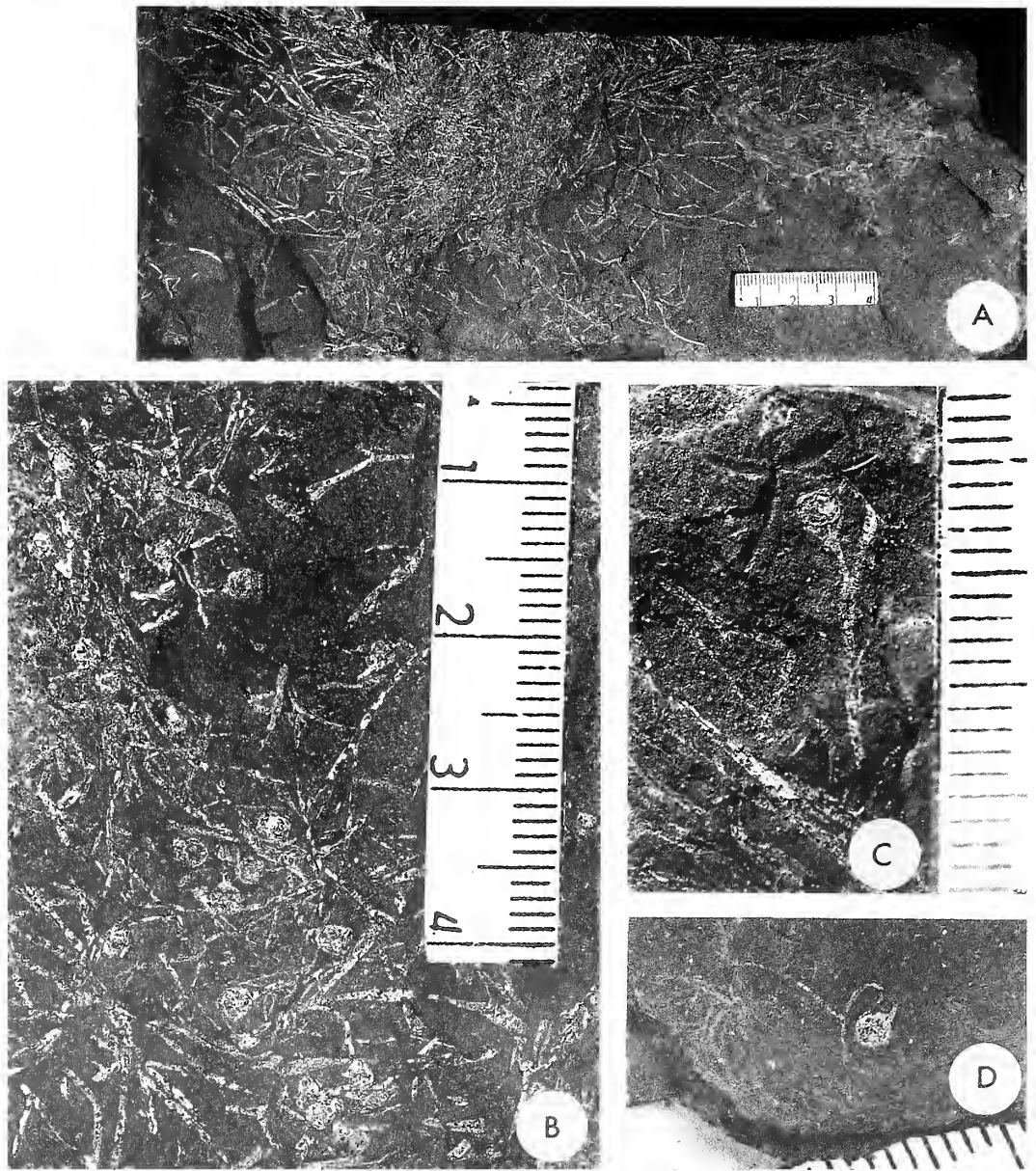


Fig. 14 A-D. Possible rhyniopsid: A. Seemingly near complete specimen; B. Detail of A; C. Sporangium attached to side of fairly proximal axis (detail of A); D. Sporangium attached to end of distal axis.

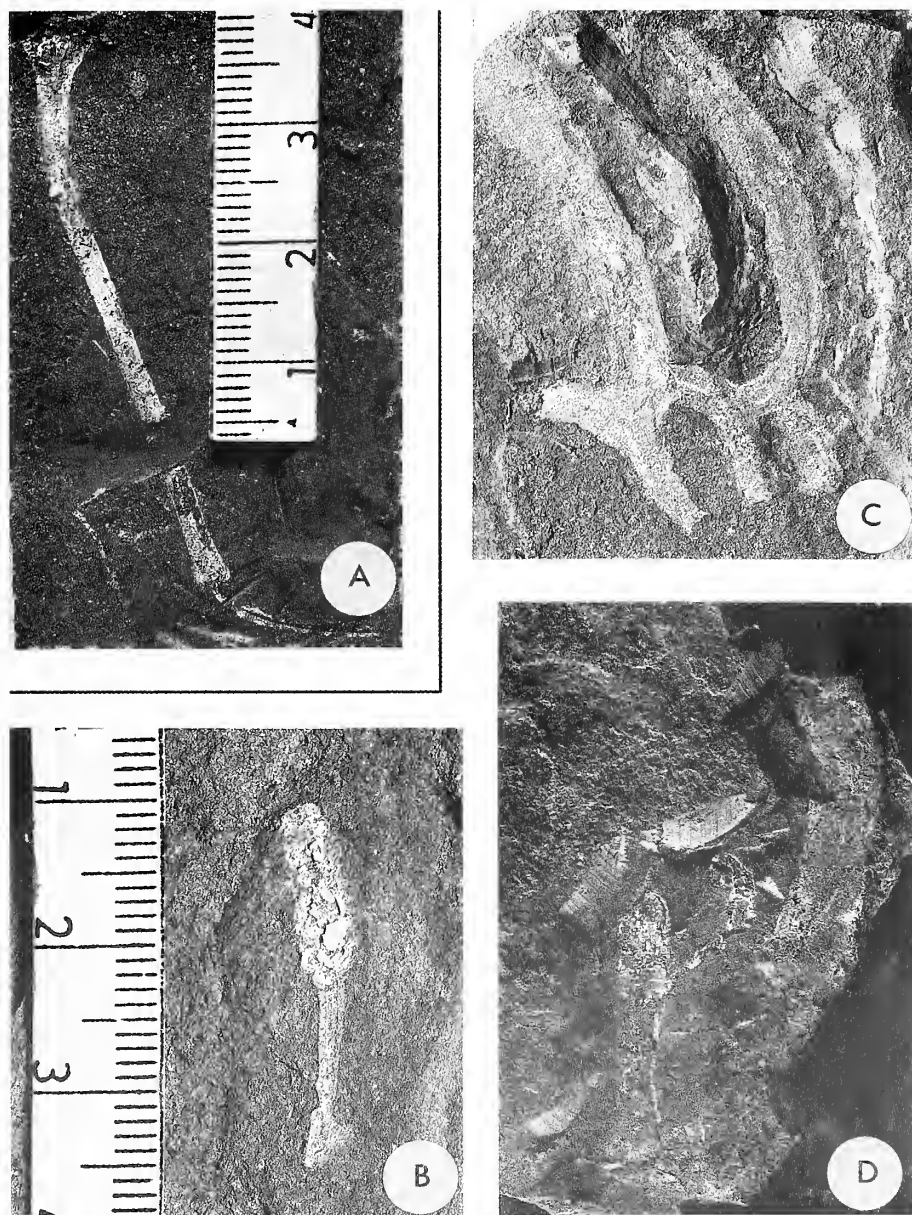


Fig. 15A-D: A. Gametophyte rhyniopsid; B-D. *Zosterophyllum*: B. Fertile spike; C. H-branching; D. K-branching.

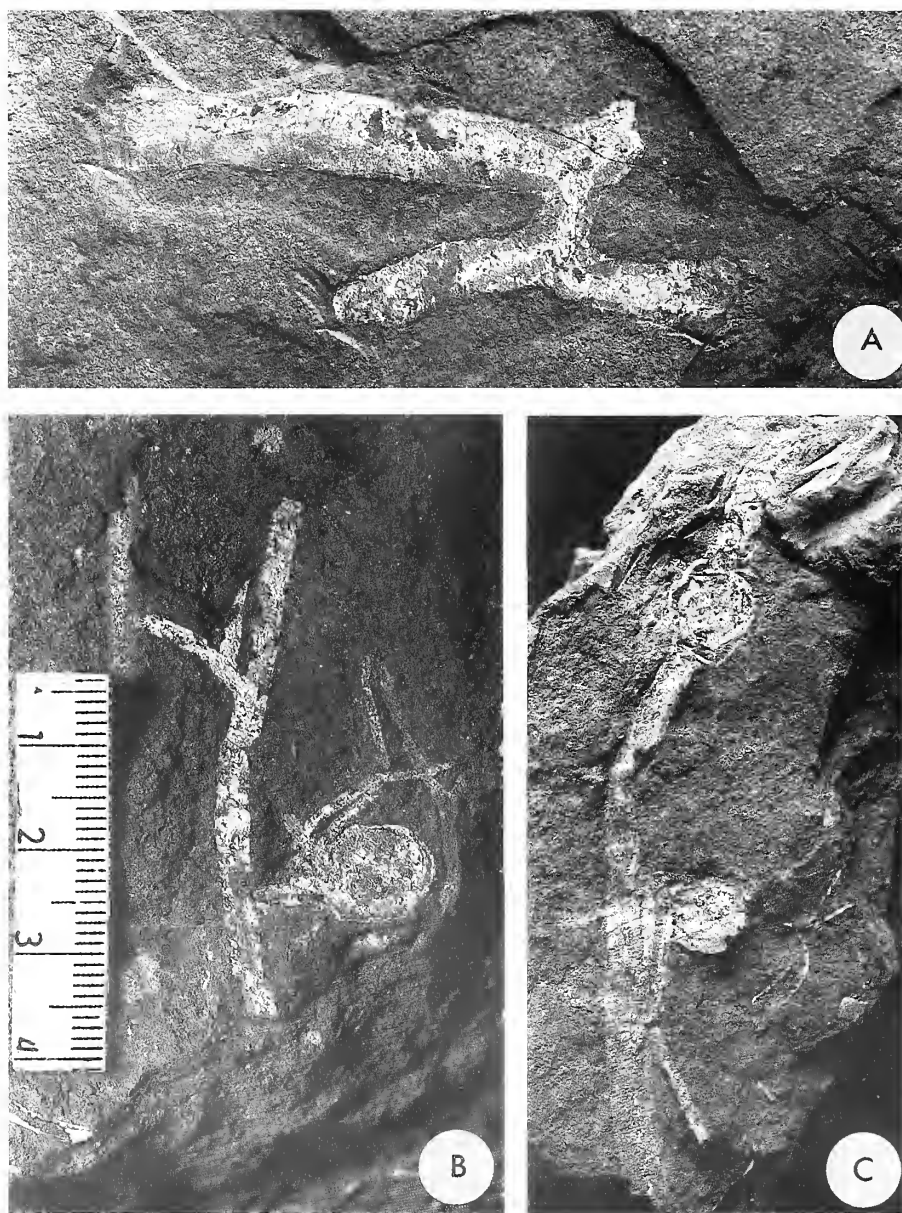


Fig. 16A-C. *Zosterophyllum*: A. H-branching; B. "Spheroid" laterally attached to rhizome; C. Two "spheroids" laterally attached to rhizome.

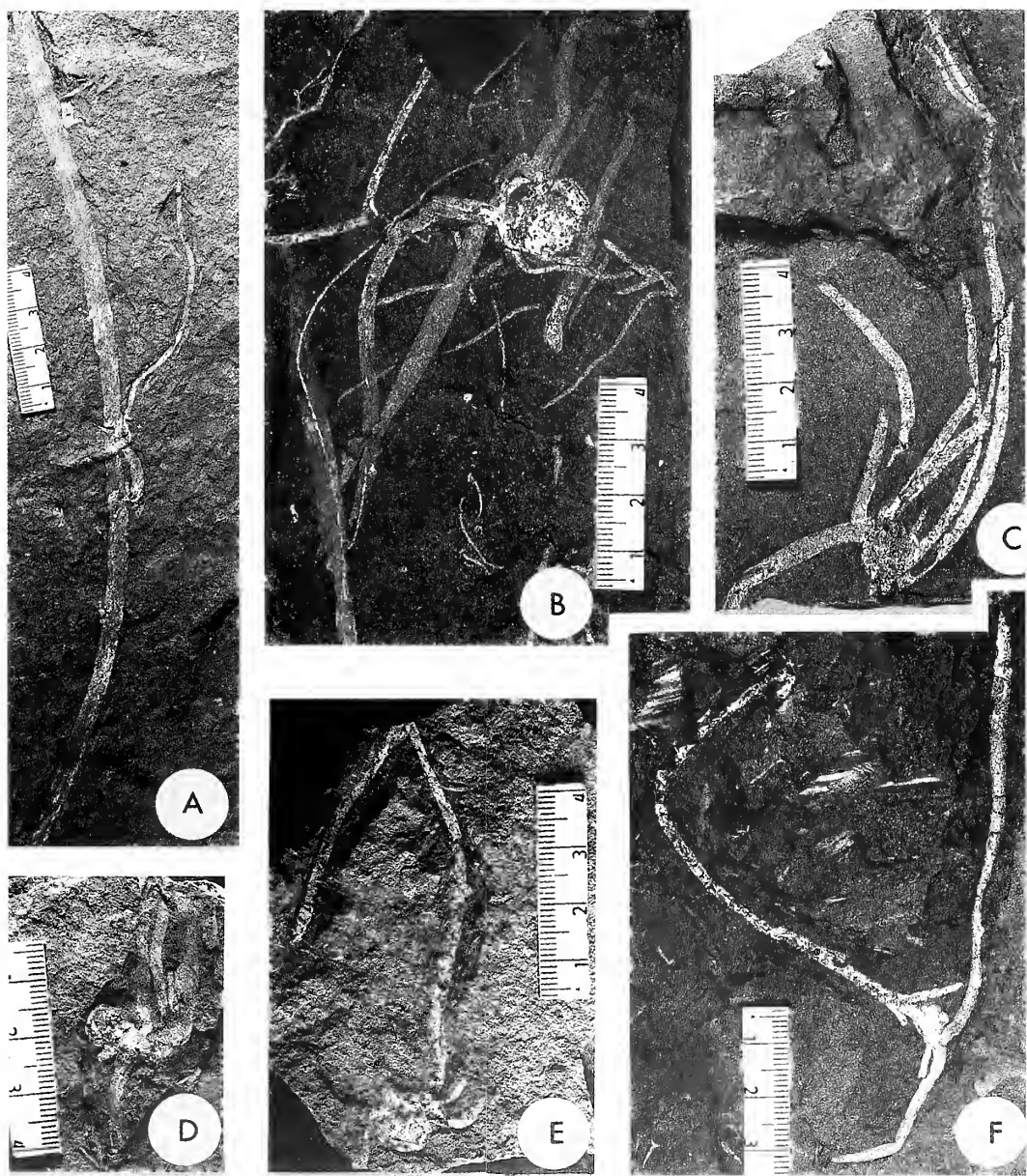


Fig. 17A-F. *Zosterophyllum*: A. ? "leaves" attached to ?rhizome; B. Rhizome, "spheroid", "leaves" and "rootlets"; C. "Spheroid" with "leaves"; D. "Spheroid" with "leaf" bases; E. "Spheroid" with "leaf" and "rootlets"; F. ? Rhizome, "spheroid", "leaves" and "rootlets".

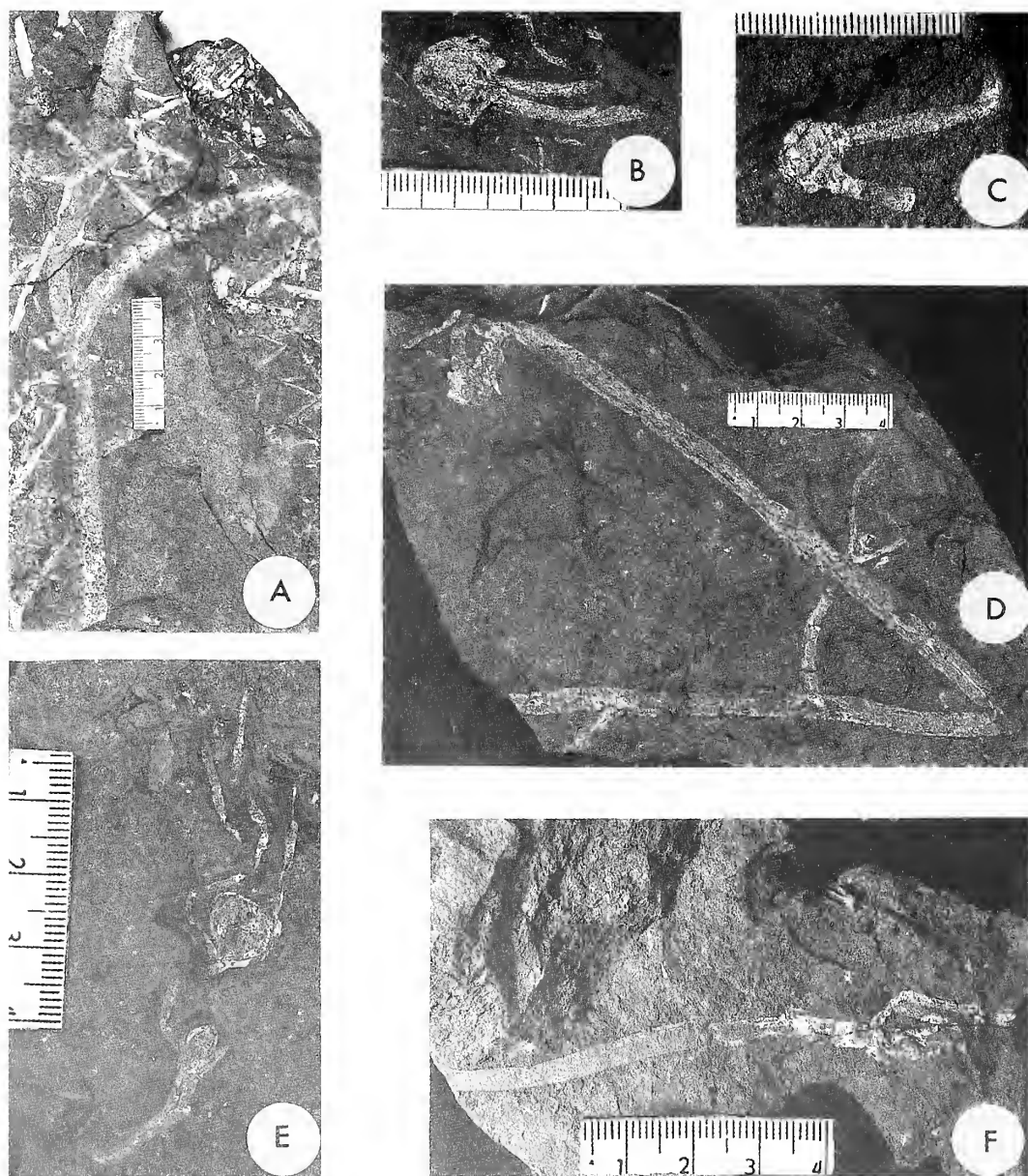


Fig. 18A-F: A. ? *Zosterophyllum*; B-C. *Zosterophyllum* "spheroids" apparently connecting two rhizomes; D-E. Unusual ? *Zosterophyllum* specimens; F. ? *Zosterophyllum* rhizome and "rootlets" from which "spheroid" has been broken.

in diameter that apparently emit “leaves” in tufts (Fig. 17B-E); they may act as anchors and/or storage organs. These “spheroids” also emit finer emanations that may anchor the tufts in the manner of rootlets (Fig. 17B). These “spheroids” were apparently connected by rhizomes as they often appear to terminate the latter (Fig. 17B-C). In some specimens they are laterally connected to the rhizomes, and probably anchored them at intervals (Fig. 16B-C). Sometimes two rhizomes are found apparently connected by the “spheroid” structures (Fig. 18B-C). These structures are reminiscent of the “corm” of the extant genus *Isoetes*.

Other material that superficially resembles rhizome material is probably unrelated. Most important is material bearing very small forked appendages and covered in “spots” (Fig. 40C), and other material displaying branching of a type uncharacteristic of *Zosterophyllum* (Fig. 40F).

Among our *incertae sedis* is a circinate specimen that may also belong to this class (Fig. 40G).

Lycopsidea (Figs 19-28, 29A-D)

Two putative herbaceous lycopsids from the site cannot be assigned with confidence to known orders. One of these is represented by fertile and infertile axes (Fig. 19). The infertile axes reach at least 80 mm in length and bear curved microphylls up to 13 mm long. The fertile axes are not completely preserved, the largest specimen being only 30 mm long. Their microphylls are very similar to those on infertile axes but they bear sporangia cradled in elongate boat-shaped cups on their adaxial surfaces. The cups extend for about one-quarter of the length of the leaves.

Much larger, though structurally similar, fertile leaves have also been collected from the site (Fig. 20). Although the full length is not preserved in any specimen, some leaves exceed 40 mm. The sporophylls are apparently unbent and thus probably do not form part of a cone. They have a narrow tapering attachment from which a midrib extends the full preserved length of each specimen. Distal to the attachment, the leaf broadens to about 6 mm, producing a protective structure for a sporangium. An extended lamina tapers narrowly towards the leaf tip. Fine hair-like fimbriations along the margins of the lamina are longest near the sporangium and extend for about one-half of the length of the leaf.

A further type of vegetative material present is not directly associated with reproductive material, and may represent herbaceous, or arborescent material. It is represented by axes that dichotomise and bear slender pointed microphylls (Fig. 21). The proximal axis, 40-100 mm long and up to 4 mm wide, divides as many as three times, giving rise to thinner axes typically extending another 100 mm. The microphylls average 3 mm in length.

Putative arborescent Lycopsidea (Figs 22-28, 29A-D)

The arborescent lycopsid *Leptophloeum australe* (McCoy (1874)) Walton (1926) is well represented in our collections as fragments of stems (Figs 22-24), some with attached roots, proximal branch segments (Fig. 22D), and possible fertile structures (Fig. 29A-C). Stems bearing roots are about 600 mm long and 45 mm wide. Above the roots (Fig. 24C-F) the epidermis is smooth for 220-270 mm; beyond this rhomboid leaf scars become visible (Fig. 24B). At about two-thirds of the way to this point the stems narrow to 30 mm. Fig. 23A-G illustrates the variation in morphology and preservation of the leaf bases of *L. australe*.

Fig. 23H shows an example of possible decortication in *L. australe*. Further material exhibiting this phenomenon is illustrated in Fig. 25, with an associated structure that may represent a shoot or fertile body (Fig. 25D,E).

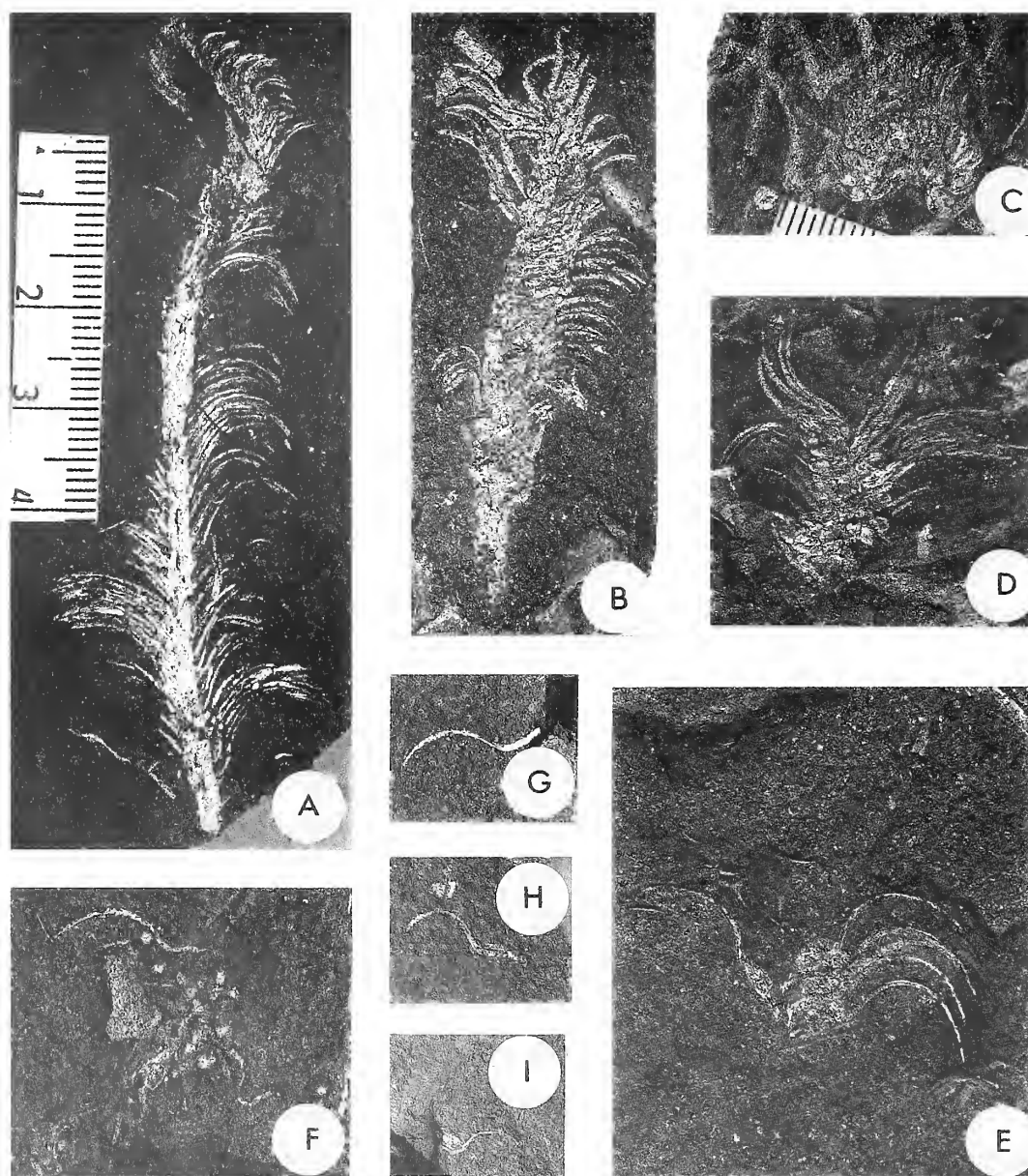


Fig. 19A-I: A Putative herbaceous lycopsid (type one) (all to same scale); A-B. Infertile axes; C-D. Apices of fertile axes; E. Microphylls from fertile axis; F. Microphylls associated with small trilete spores; G. Infertile microphyll; H. Fertile microphyll without sporangium; I. Fertile microphyll with sporangium.

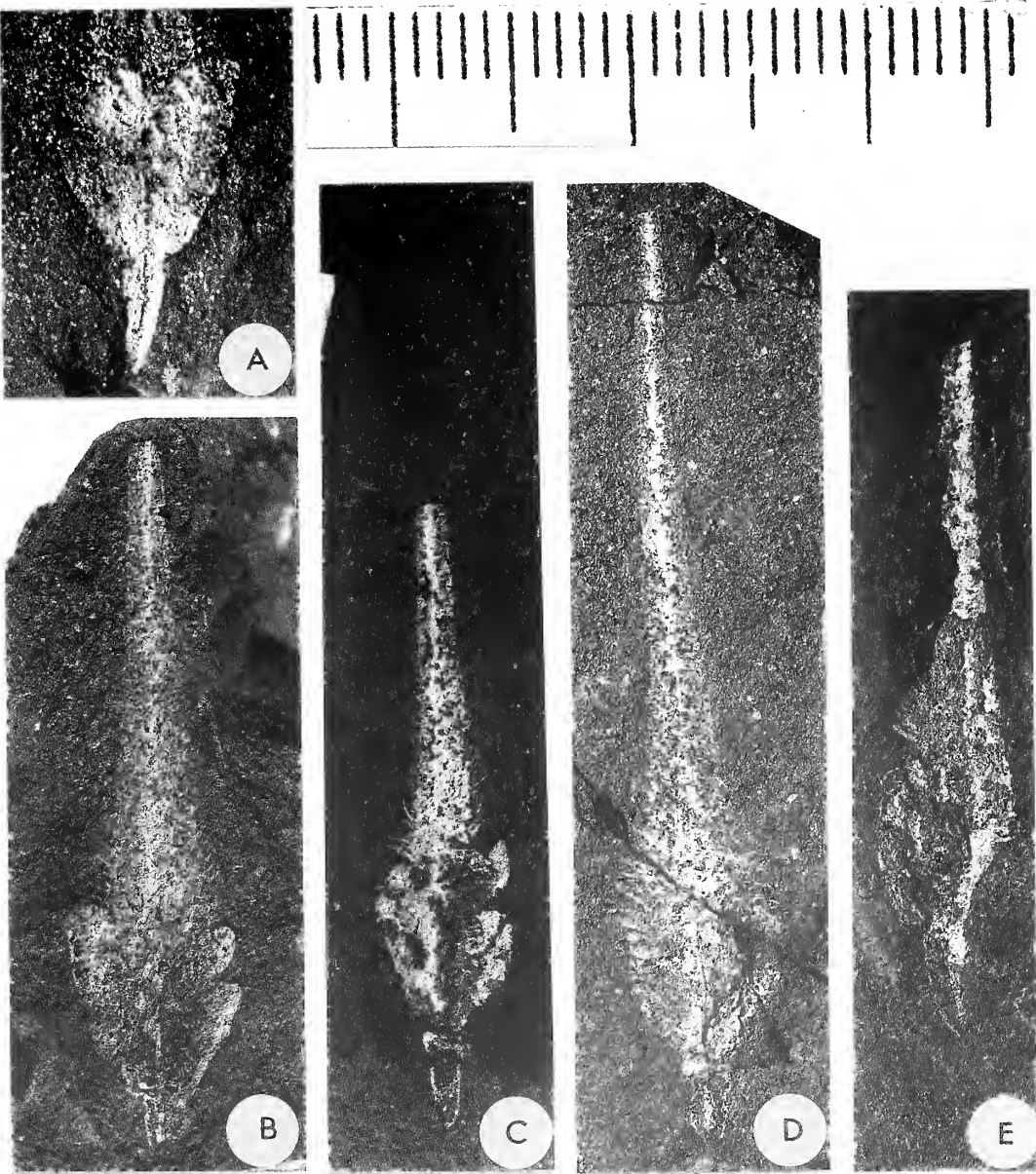


Fig. 20A-E. Putative herbaceous lycopsid (type two) (all to same scale) fertile microphylls.

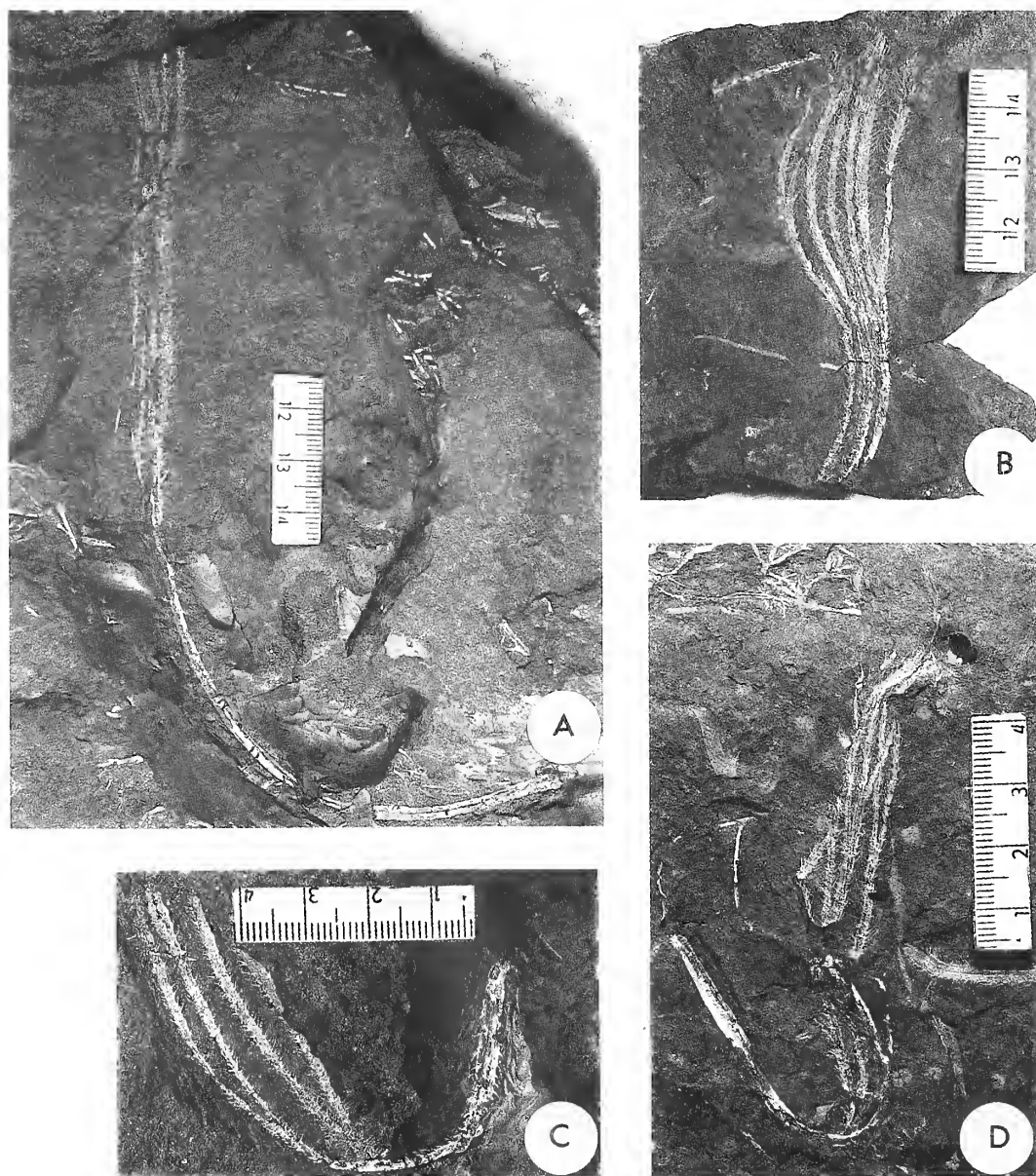


Fig. 21A-D. Infertile lycopsid axes bearing microphylls.

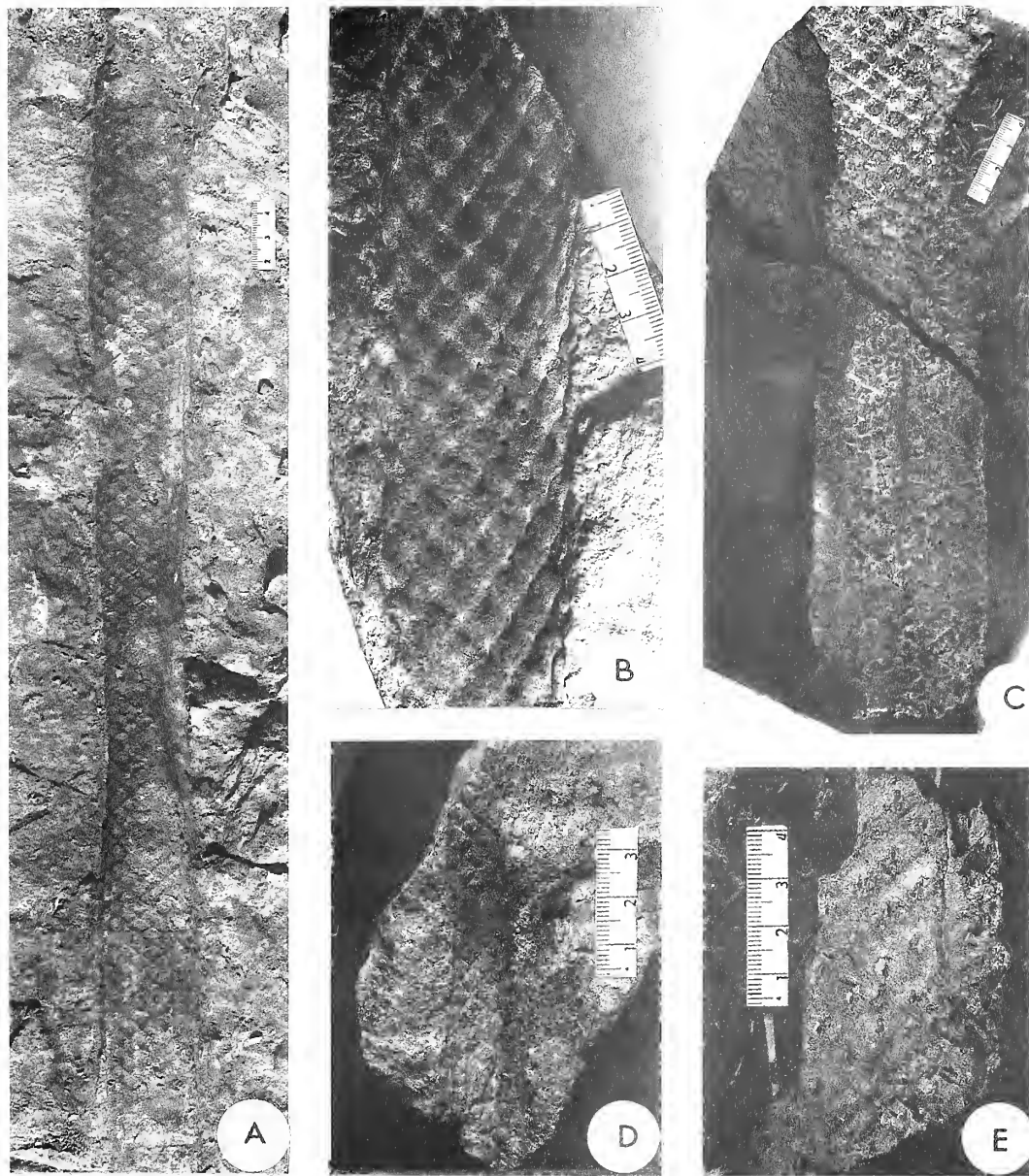


Fig. 22A-E. *Leptophloeum australe* (McCoy) Walton: A. Stem from mud chip conglomerate lens; B. Stem from sandstone displaying leaf impressions; C. Stem from black shale; D. Portion of branch from mud chip conglomerate lens; E. Stem from black shale displaying preferential preservation of leaf impressions.

Material displaying spirally arranged, closely spaced, elongate leaf scars (Fig. 26 A-C) is tentatively assigned to the form genus *Longicatrix* Anderson and Anderson (1985). The authors do not, however, exclude the possibility that the material could represent the decorticated inner core of an arborescent lycopsid such as *L. australe*.

A single specimen displays the distinctive hexagonal leaf scars characteristic of *Archaeosigillaria* Kidston (1901) (Fig. 26D), most closely resembling *Archaeosigillaria caespitosa* (Schwarz (1906)) Plumstead (1967).

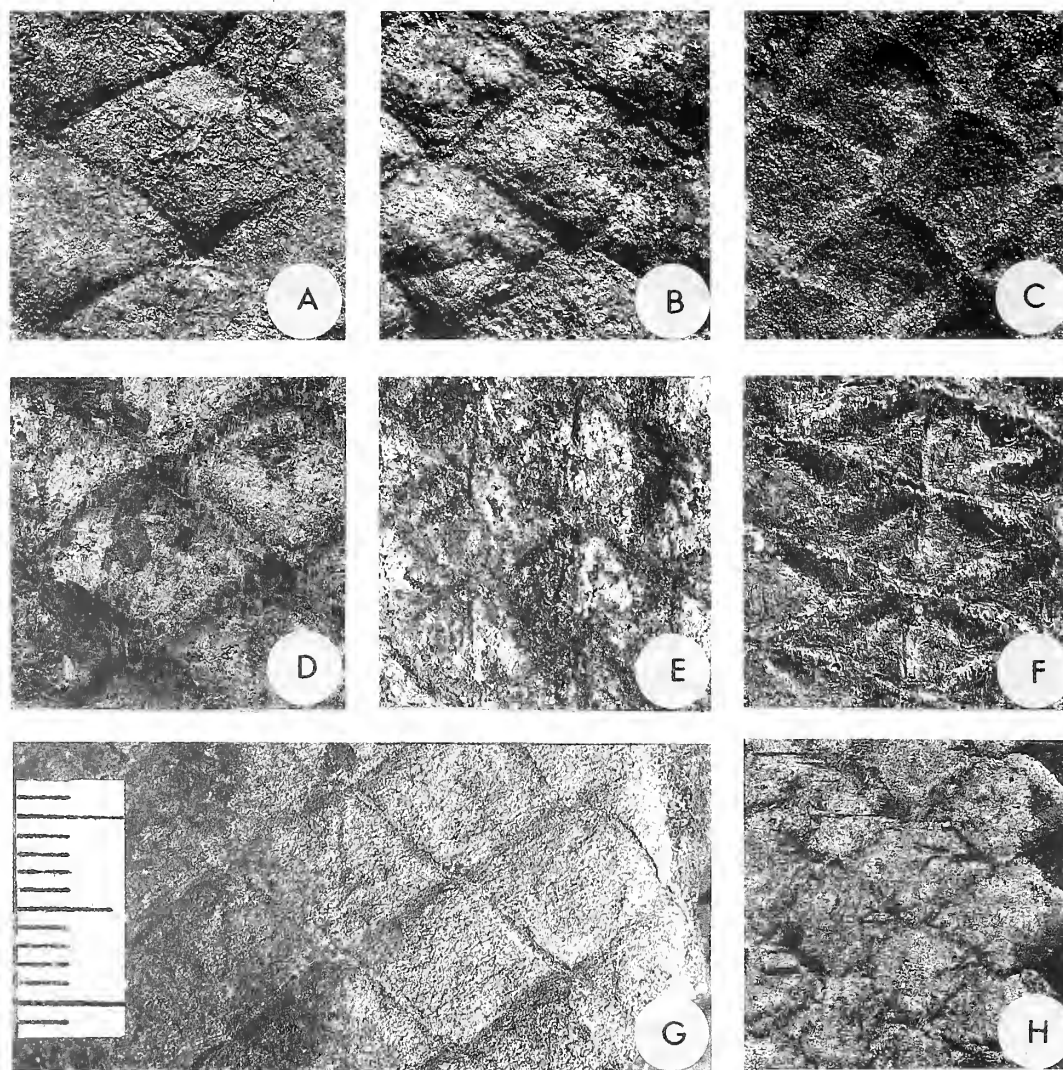


Fig. 23A-H: A-G. *Leptophloeum australe* (McCoy) Walton displaying variation in rhombic leaf bases, and preservation thereof: A-C. From mud chip conglomerate lens; D-G. From black shale; H. ? Decorticated *Leptophloeum* from black shale.

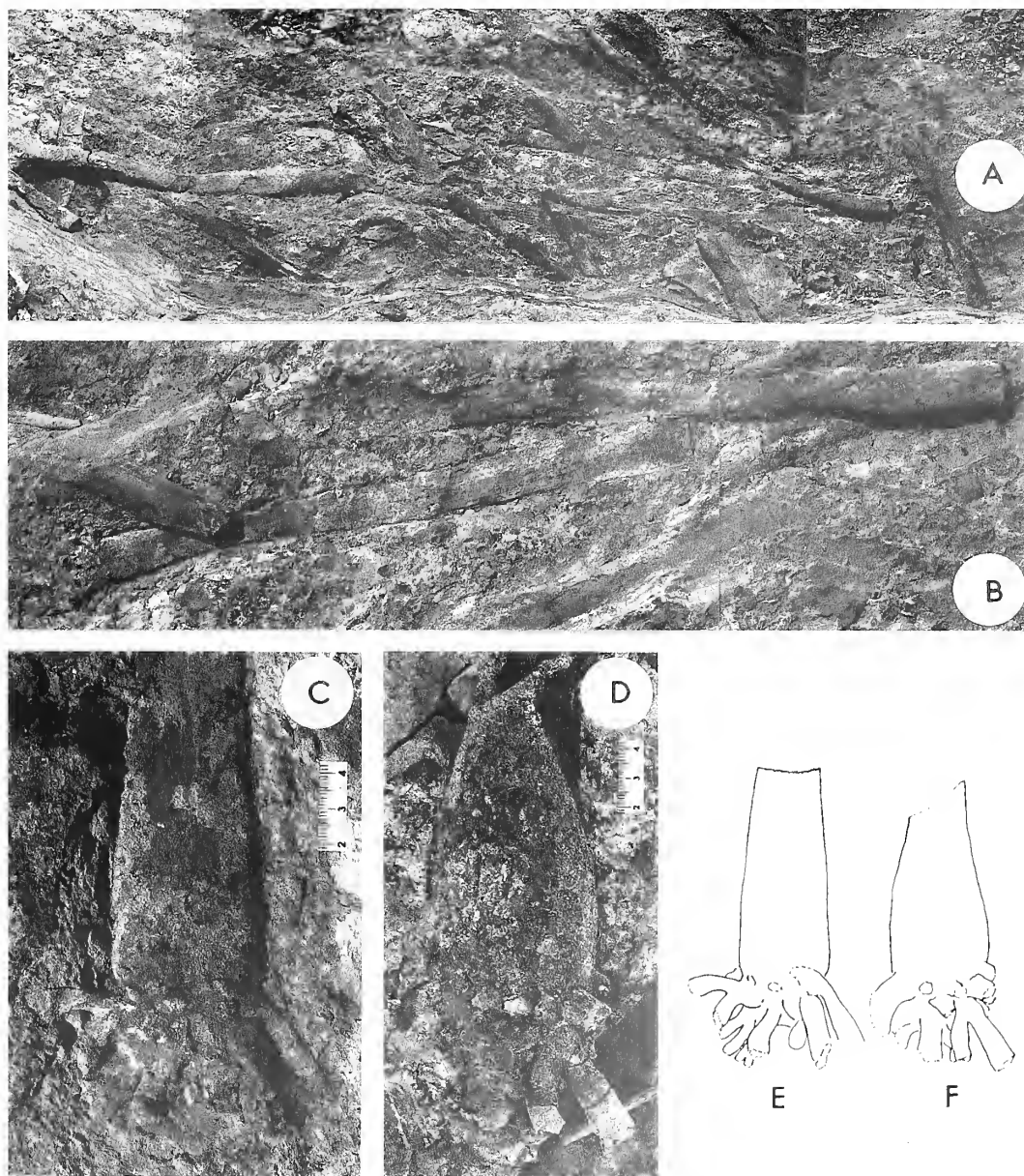


Fig. 24A-F. *Leptophloeum australe* (McCoy) Walton from mud chip conglomerate lens: A. *In situ* excavation of stems; B. Two stems bearing root bases (external mould in top specimen); C-D. Close up of root bases; E-F. Clarification of C and D.

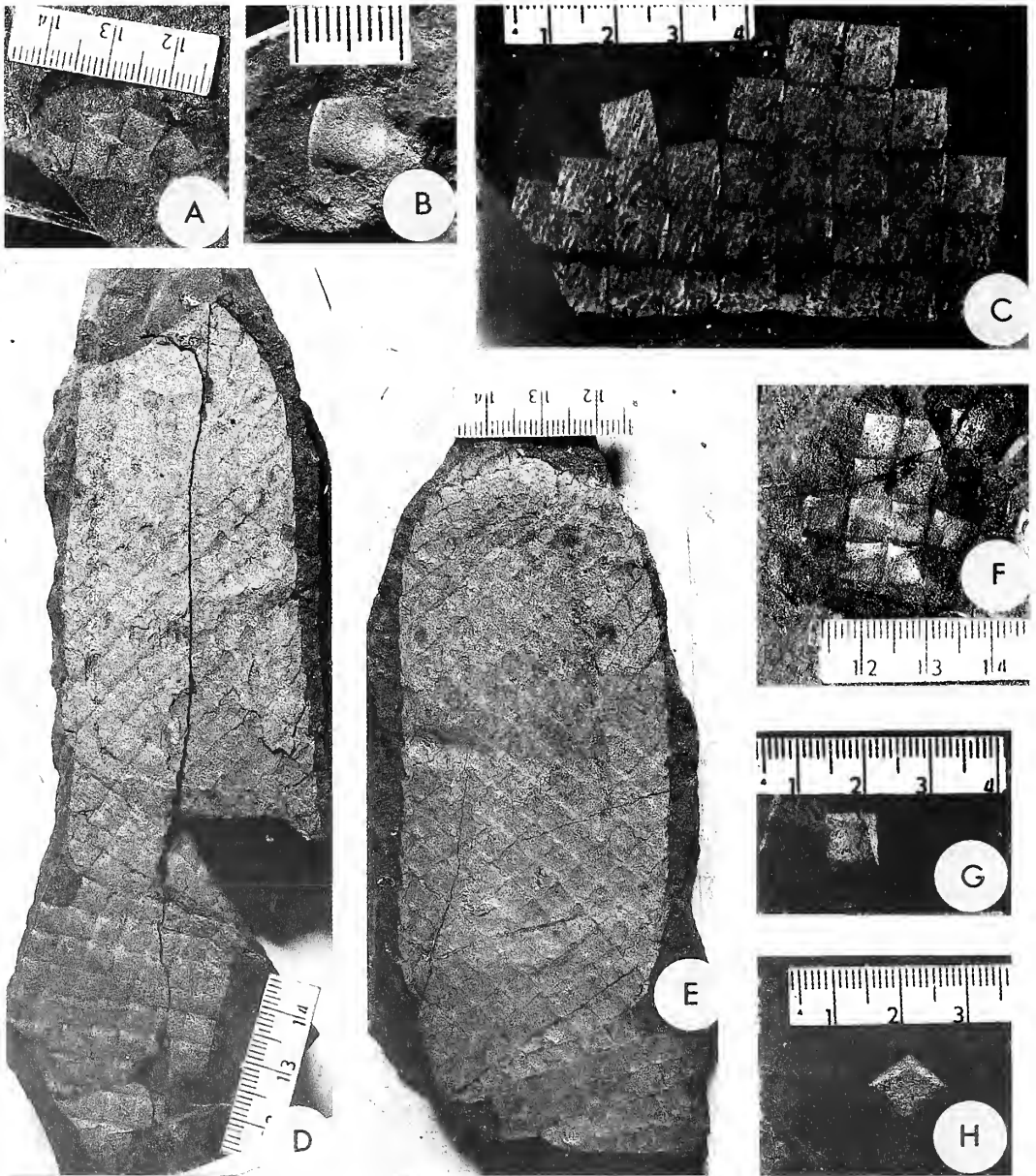


Fig. 25A-E. ? *Leptophloeum australe* (McCoy) Walton: A-C, F-H. ? Outer cortex; D-E. ? Shoot or fertile structure.

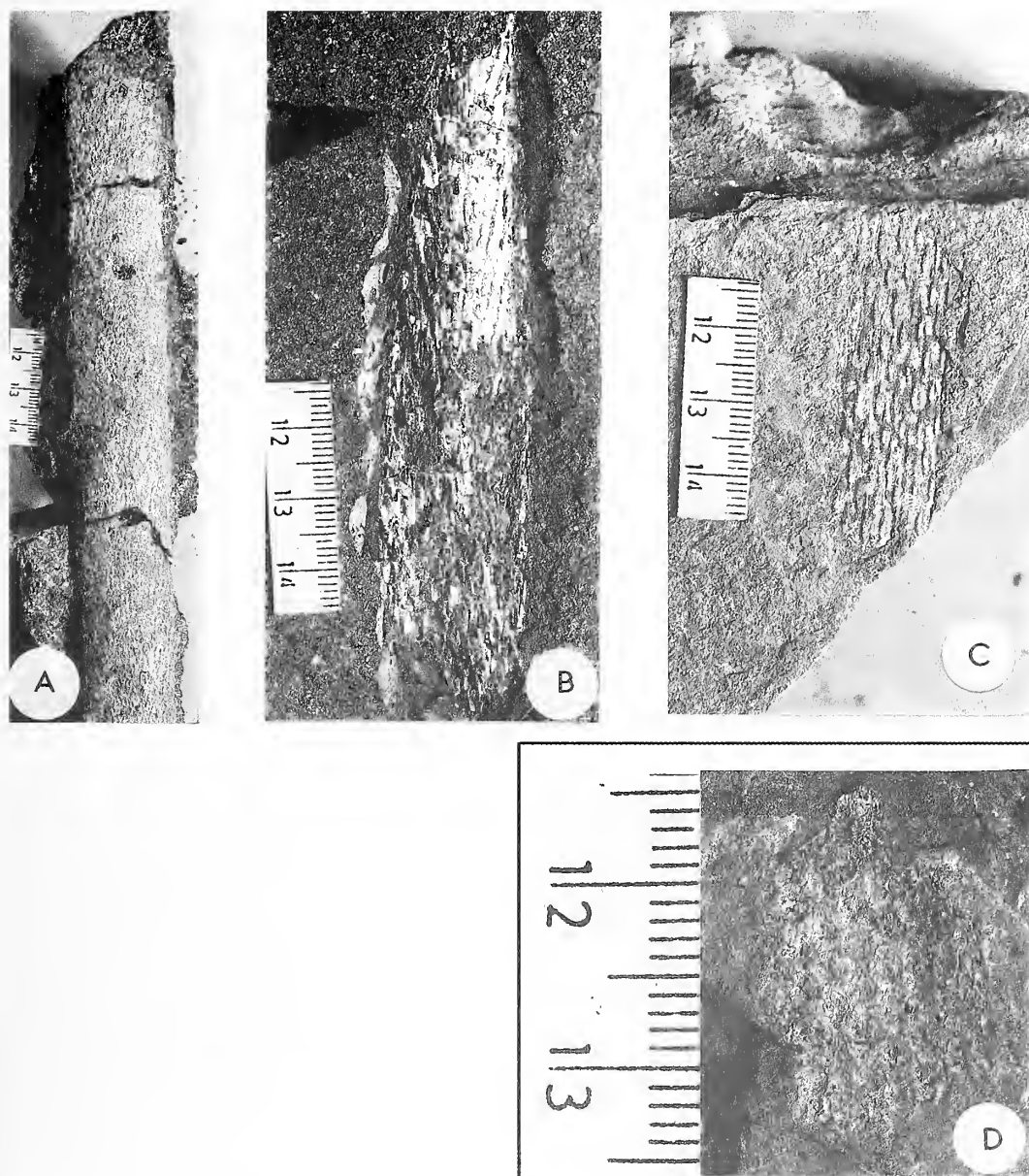


Fig. 26A-D: A-C. *Longicatrix* Anderson and Anderson; D. *Archacosigillaria* Kidson.

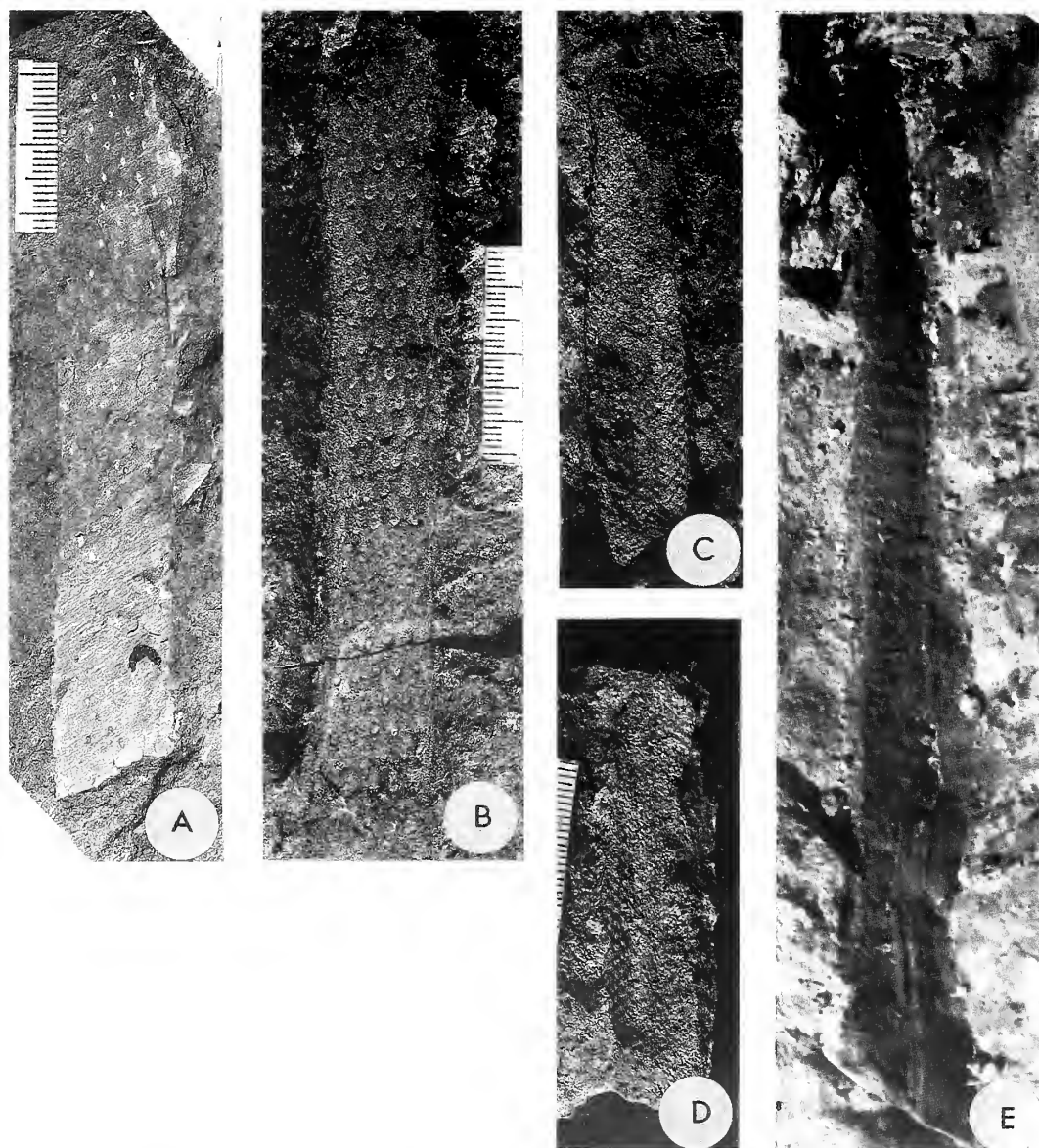


Fig. 27A-E. *Haplostigma irregularis* (Schwarz) Seward; A. From black shale; B-E. From mud chip conglomerate lens.

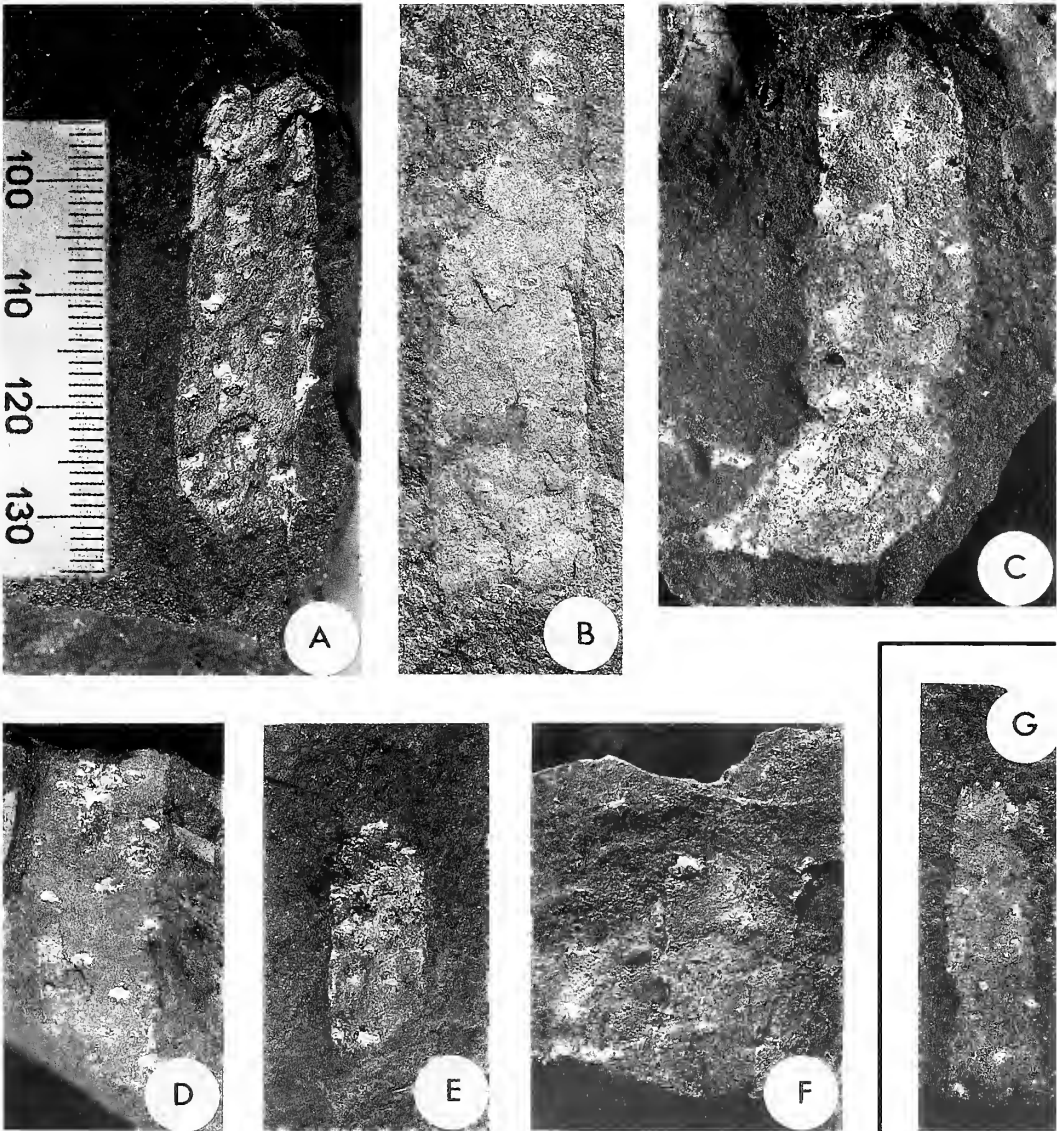


Fig. 28A-G: A-F. *Palaeostigma robusta* Anderson and Anderson; G. ? *Palaeostigma*

Haplostigma irregularis (Schwarz (1906)) Seward (1932) has been recovered from the black shale (Fig. 27A) as well as from the mud-chip lens (Fig. 27B-E). In the lens it is associated closely, and exclusively, with the stems and subaerial portions of young *Leptophloeum australe*. Plumstead

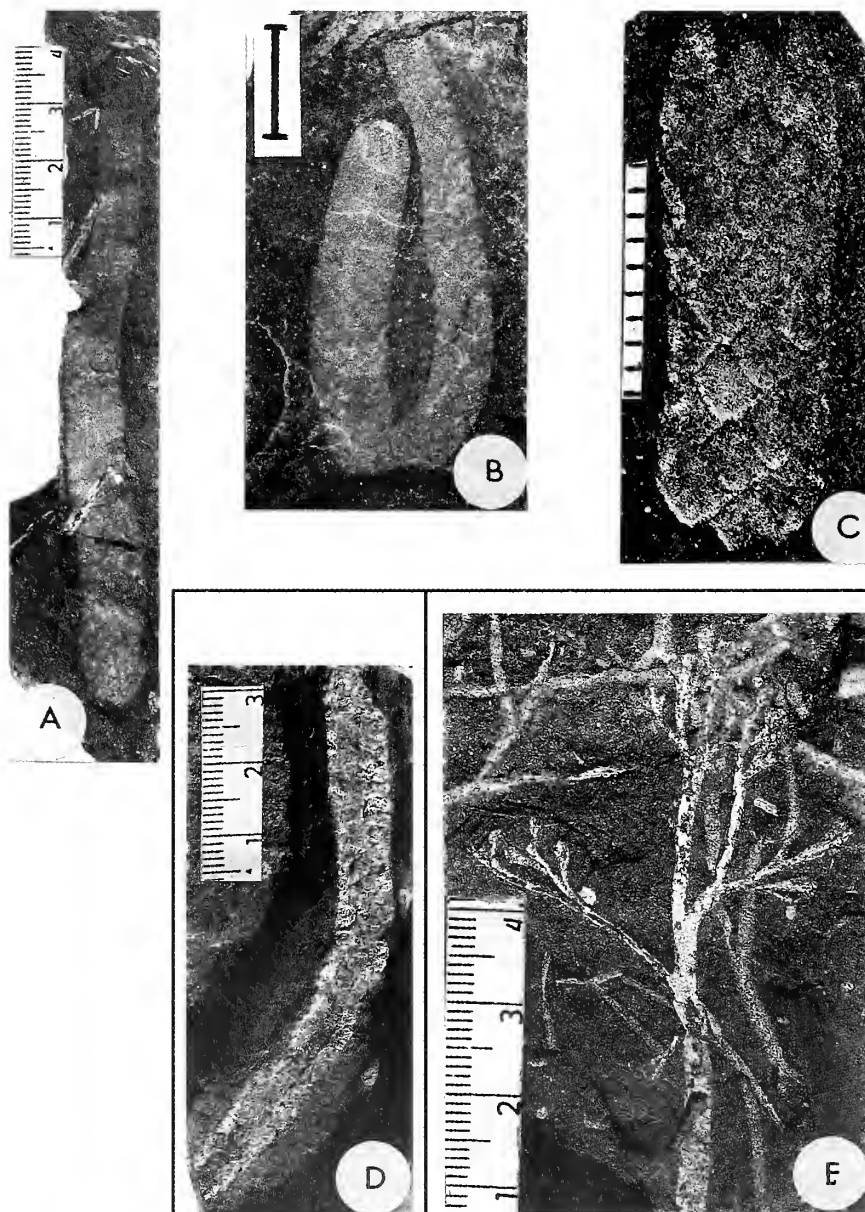


Fig. 29A-E: A-C. ? *Leptophloeum australe* (McCoy) Walton cones; D. ? Arborescent lycopsid cone; E. ? Trimerophyte reproductive material.

(1967) commented on the frequent association of these two axial types and suggested that *Haplostigma* may represent younger twigs of *Leptophloeum*. However, the material described here contains a rhombically scarred axis narrower than many of the *Haplostigma* axes associated with it (Fig. 22D). In addition, fine twigs of *L. australe* reported from Australia (White 1990, p.76), do not possess round scars, but rather resemble the specimen figured in Plumstead (1967, pl. XIV-8). The authors believe that the *Haplostigma* material in their collection probably represents the roots of *L. australe*. The authors also assume that their associated *Haplostigma* material all belongs to the same species, despite the similarity of some specimens to *H. kowiensis* (Plumstead (1967)) Anderson and Anderson (1985).

Palaeostigma robusta Anderson and Anderson (1985) from the site (Fig. 28A-F) is nearly identical in morphology and preservation to material recorded from the Howison's Poort site.

Various long, narrow, cone-like structures (Fig. 29A-C) are presumed to represent the reproductive structures of an arborescent lycopsid, possibly *L. australe*.

cf. Trimerophytosida (Fig. 29E)

A single, possibly reproductive specimen has a gross morphology that suggests trimerophyte affinities (Fig. 29E). Seven centimetres of a terminating axis are preserved displaying alternate branching. The first branch arises after 3.2 cm and the next after a further 1 cm. The branches divide a further two to three times before terminating in expansions.

Class indeterminate *cf. Calamophyton* (Fig. 30A-C)

A reproductive truss believed to be from a plant of the *Calamophyton* type (Fig. 30A) has been recovered. It is not associated with any sterile material, but we believe that some axes from the site that display short lateral extensions could belong to this plant (Fig. 30B-C).

Progymnospermopsida (Figs 30D-H, 31-38)

Of the large amount of material collected that probably is assignable to this group, most can be assigned to four species. Additional material of note includes arborescent axes (Fig. 30H) that as yet have not been unequivocally correlated with finer axes. Some of this material possesses outgrowths containing a central vascular strand that may represent roots (Fig. 41F). Various isolated leaf-like structures have also been collected (Fig. 30D-G).

Archaeopteris sp. (species description by Anderson *et al.*, in press) occurs in both the main shale horizon and a thin shale interbedded with the sandstone a little lower in the sequence (Fig. 2A). It is noteworthy as the first confirmed *Archaeopteris* from southern Africa. The material (Figs 31-33) consists predominantly of infertile axes, fronds and frond fragments, but one fertile specimen has been found (Fig. 32C). "Pinnules" are quite variable (Fig. 33), and occur attached to both "rachises" (Fig. 32B) and "pinnae" (Fig. 33D). Towards the base of the "rachis" "rachial pinnules" are modified into small bract-like structures (Fig. 31, top right).

Material that may represent another species of *Archaeopteris* is present, but consists purely of non-fertile material (Fig. 34). This consists of specimens interpreted as "pinnae" and one (Fig. 34E) in which putative "pinnae", up to 90 mm long and 2 mm wide, are connected to a portion of an apparent "rachis", 65 mm long and 4mm wide. The putative "pinnules" are up to 10 mm long, are unwebbed and divide as many as three times, once proximally, again at about mid-length, and finally near the tip. A possible third species is represented by only two specimens (Fig. 41A).

The second well represented species (Figs 35-37) has fertile material which (Figs 36A-B, F-G; 37A) is very like that of *Chauleria*. It consists of small branches that bifurcate twice to produce four recurved terminal axes, each bearing a small double pendulous structure. These structures were described from the Howison's Poort site as *Dutoitia maraisia* by Plumstead (1967), who believed them to be psilophytes. The discovery of these structures associated with several orders of woody branching has led the authors to believe that this species should be excluded from *Dutoitia*. The higher order axes found (Figs 35; 36A) are generally 5-9 mm across and show preserved lengths up to 500

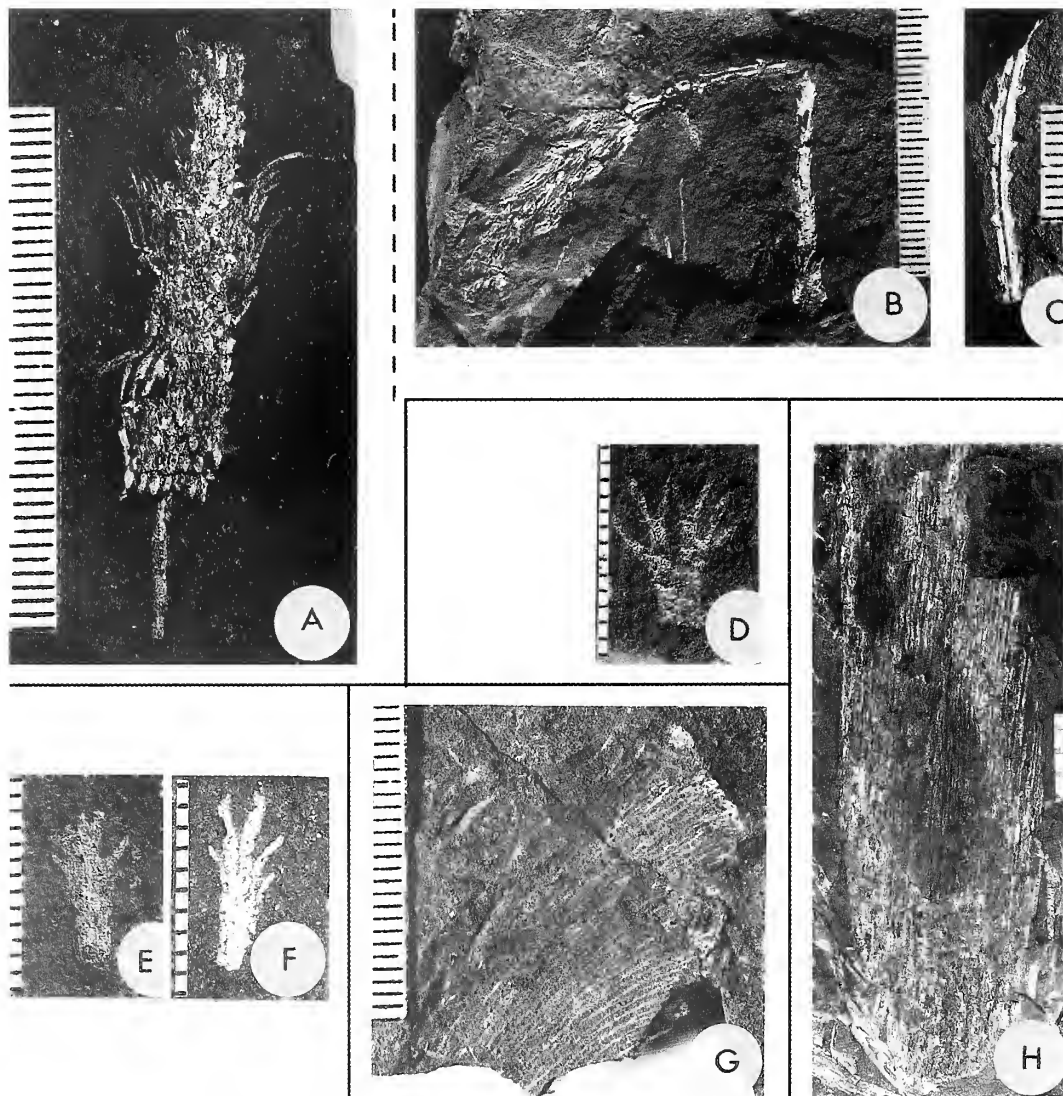


Fig. 30A-H: A. *cf. Calamophyton* reproductive head; B-C. *cf. Calamophyton* axes; D-G. Isolated leaves; H. Progymnosperm type arborescent axis.

mm. An apparent striation may represent impressions of internal vascular material. The parallel arrangement of these axes in our most complete specimen (Fig. 35) suggests that they branched off a yet larger axis.

These axes give rise at irregular intervals to "secondary axes" that are borne in fans of at least five arranged around a bud-like structure (Fig. 36C-E). Such fans may be spirally arranged on the "primary axis". The "secondary axes" are 2-5 mm across and show preserved lengths of up to 200 mm. "Tertiary axes" give rise to further branchlets that bear the fertile organs (Fig. 36F).

Associated with some specimens of this species we have found axes bearing tuft-like structures that may represent terminal (Fig. 37B) or adaxial (Fig. 37C) growth points. Other branches carry small leaf-like structures comprising very fine axes that bifurcate twice. These lack sporangia and may represent the non-fertile material of this species (Fig. 37D).

Axes described by Anderson and Anderson (1985) from Howison's Poort as *Praerumunculus alternatiramus* are almost certainly of the "secondary axis" type described above. McLoughlin and



Fig. 31. Specimen of *Archaeopteris* new species from a thin shale interbed, showing a "frond" tip, bract-like basal "rachial pinnae" (top right), and normal "rachial pinnae" (bottom right).

Long (1994) have recorded this form species from Antarctica, in association with *Haplostigma lineare*, *Malanzania* sp. and *Archaeosigillaria* cf. *A. caespitosa*. Comparison with their fragment would, however, be hazardous.

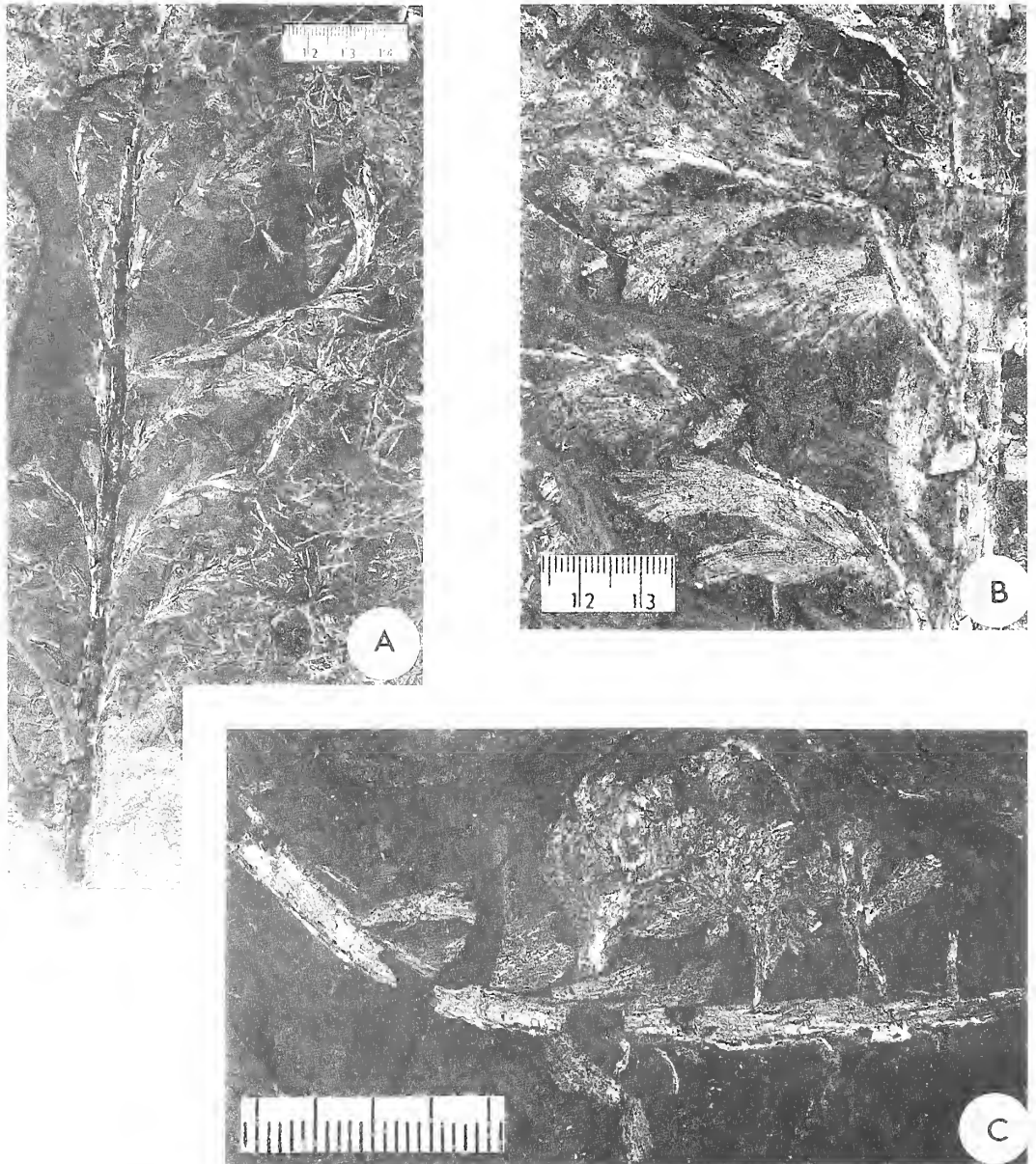


Fig. 32A-C. *Archaeopteris* new species: A. Near complete "frond" from the main black shale; B. "Pinnae" and "pinnules" attached to a "rachis", from the thin shale interbed; C. Piece of "rachis" with "rachial pinnules" and fertile material from the main black shale.

The final type of putative progymnospermous material is less well represented than the previous two. It consists of thin axes, about 1 mm across, that alternately bifurcate unequally at intervals of about 40 mm (Fig. 38A). The thinner of the two daughter branches averages about 50 mm in length and subdivides profusely before terminating in small expanded tips. Arranged around the point of unequal bifurcation are other fine axes that terminate in the same way (Fig. 38A, B, D).

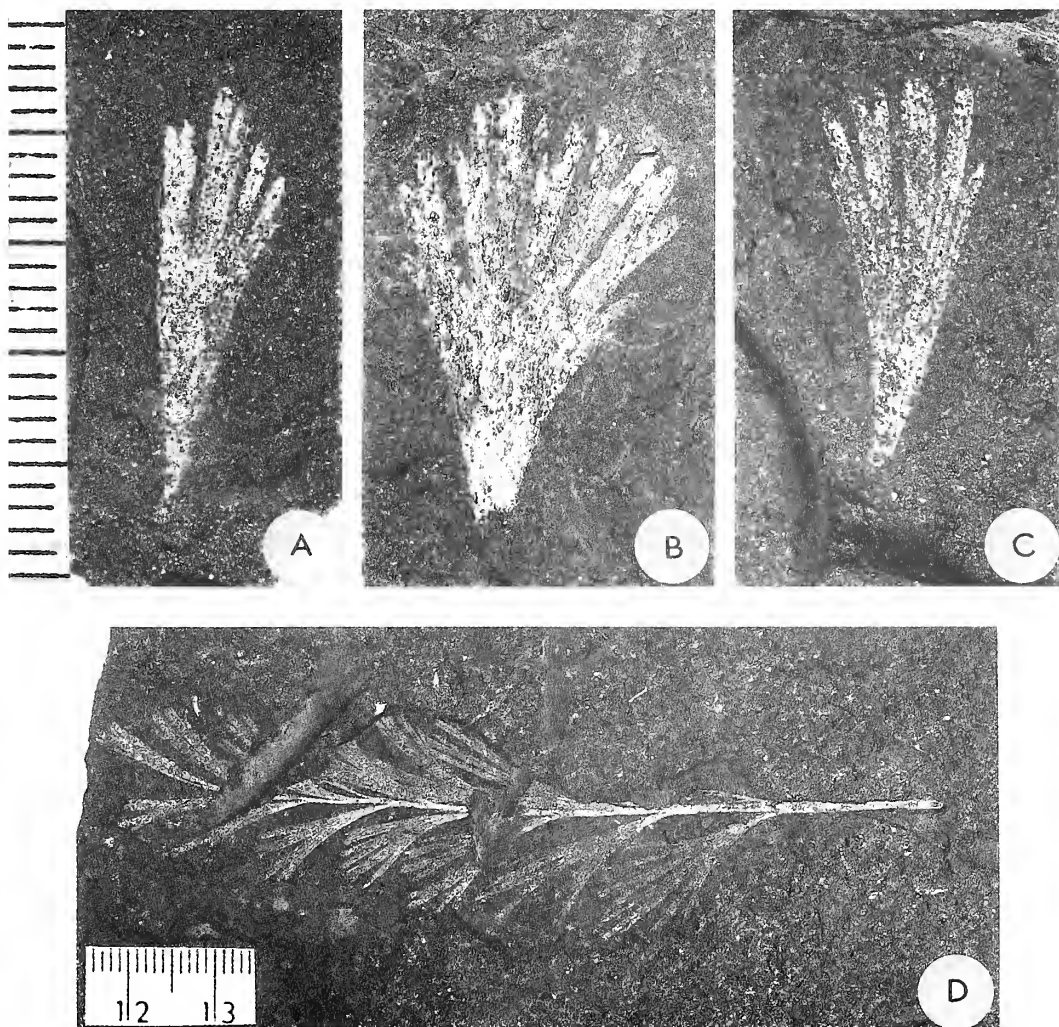


Fig. 33A-D. *Archaeopteris* new species: A-C. Isolated "pinnae" from the main black shale; D. Isolated "pinnule" from the main black shale.

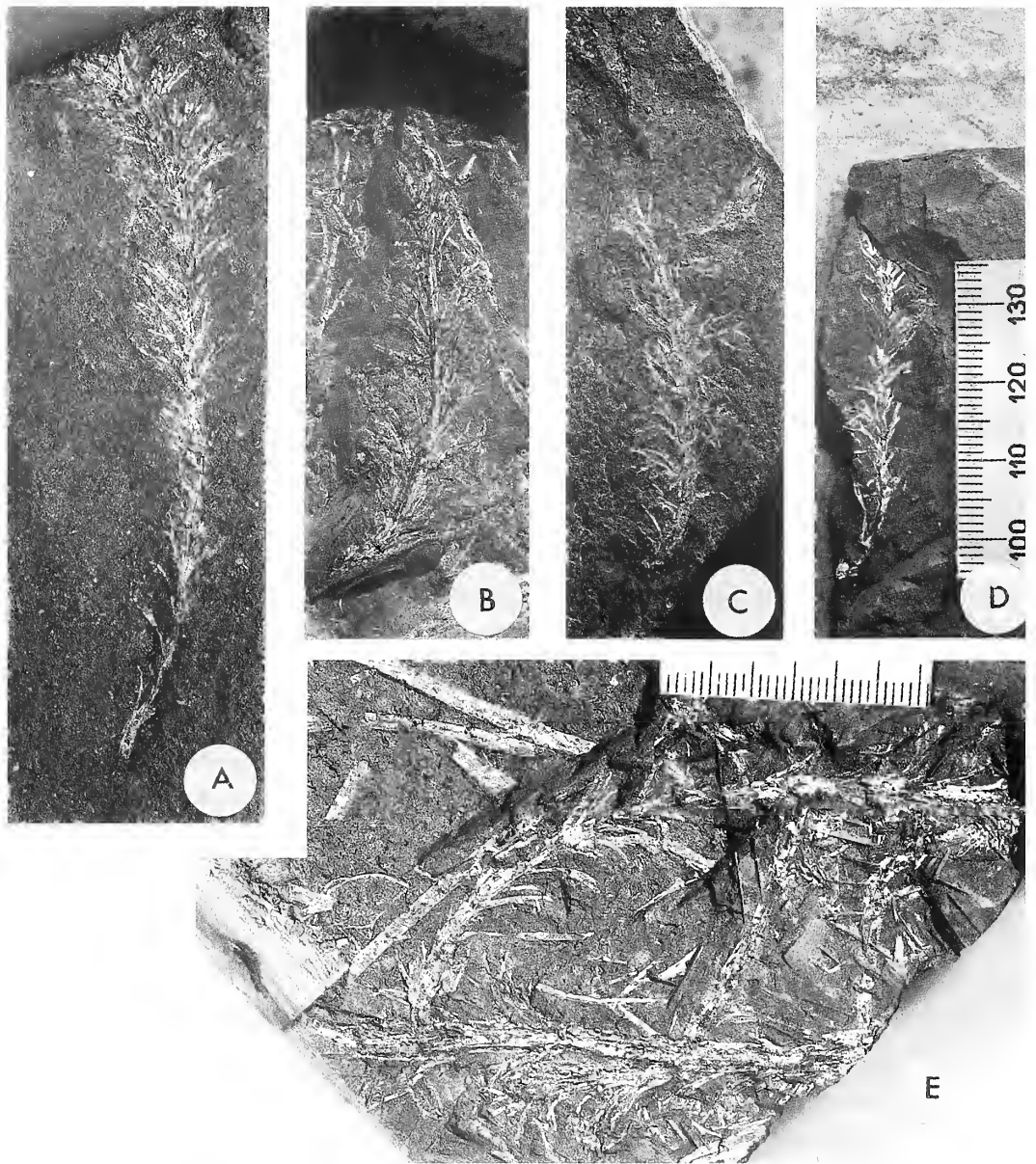


Fig. 34A-E. ? *Archacopteris* sp.: A-D. ? "Pinnules"; E. ? "Pinnules" associated with portion of "rachis".



Fig. 35. "*Dutoitia*" *maraisia*.

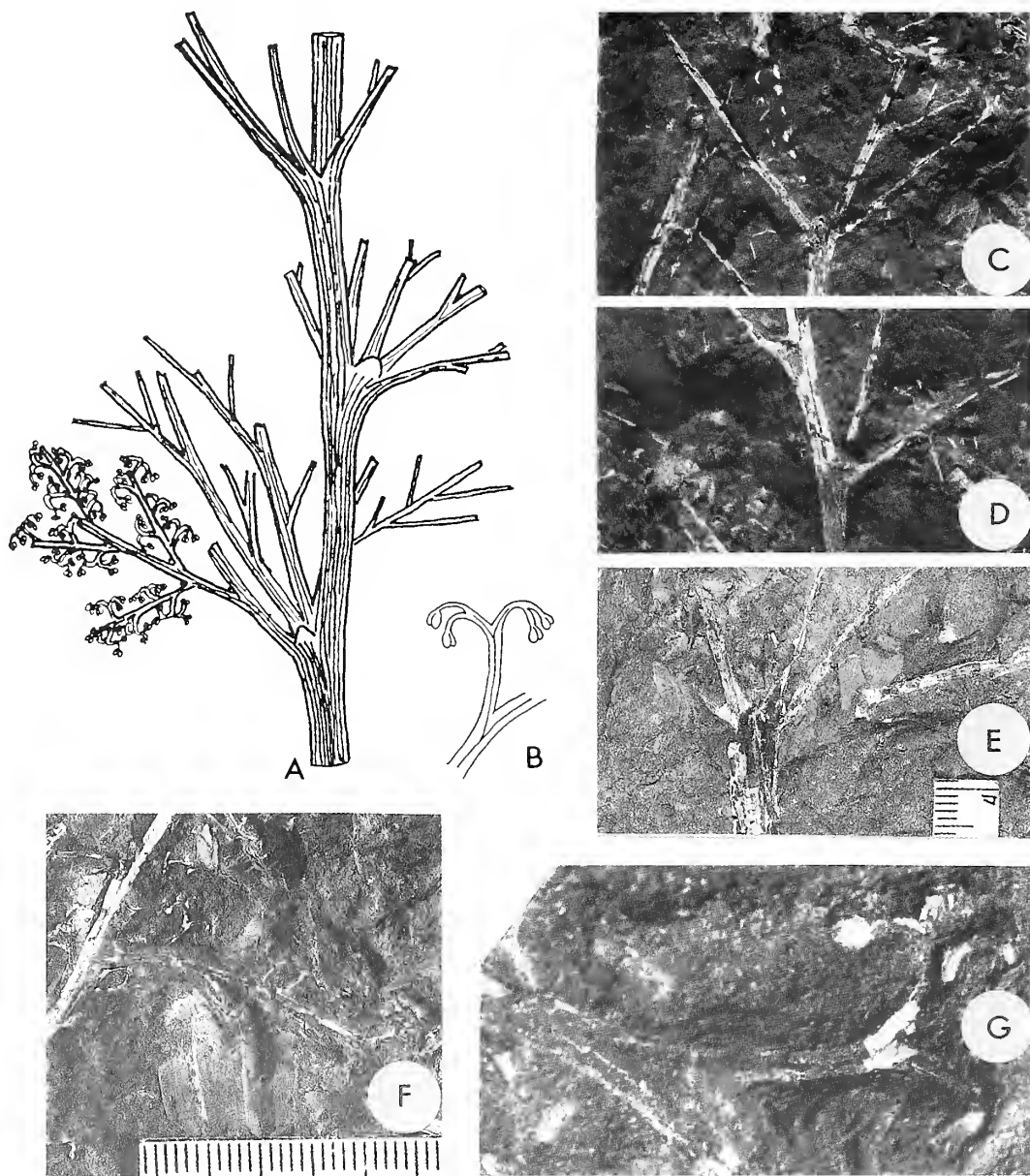


Fig. 36A-G. "*Dutoitia*" *maraisia*: A. Reconstruction of branching system; B. Reconstruction of fertile structure; C-E. Examples of "fan-like" branching; F. Fertile material attached to "quaternary branch"; G. Detail of a fertile structure in F.

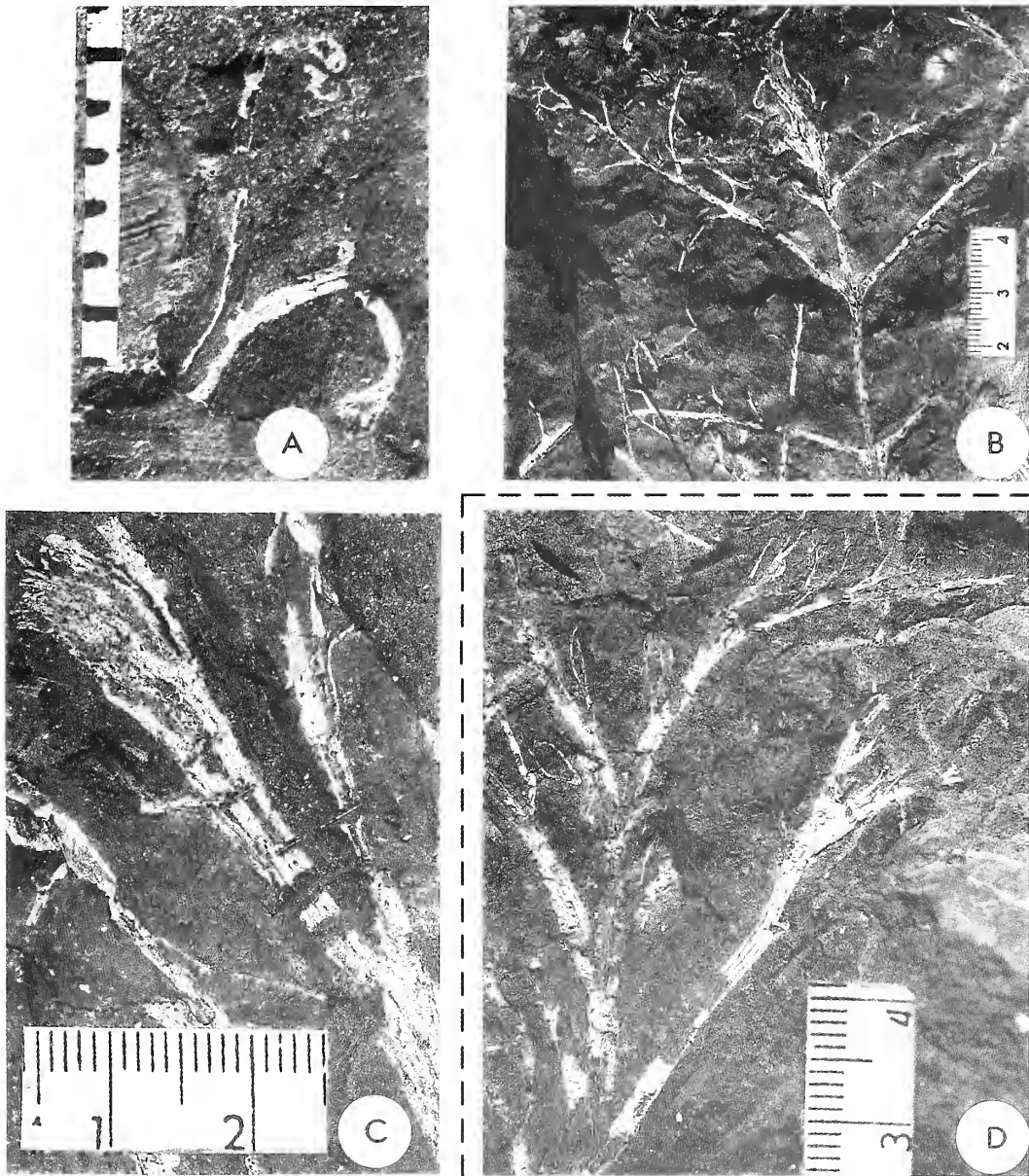


Fig. 37A-D: A-C. "*Dutoitia*" *maraisia*: A. Detail of fertile structure, B. Terminal tuft-like growth point, C. Adaxial tuft-like growth point; D. Probable leaves of "*Dutoitia*" *maraisia*.

Incertae sedis

A large number of other reproductive and vegetative specimens from the site cannot be

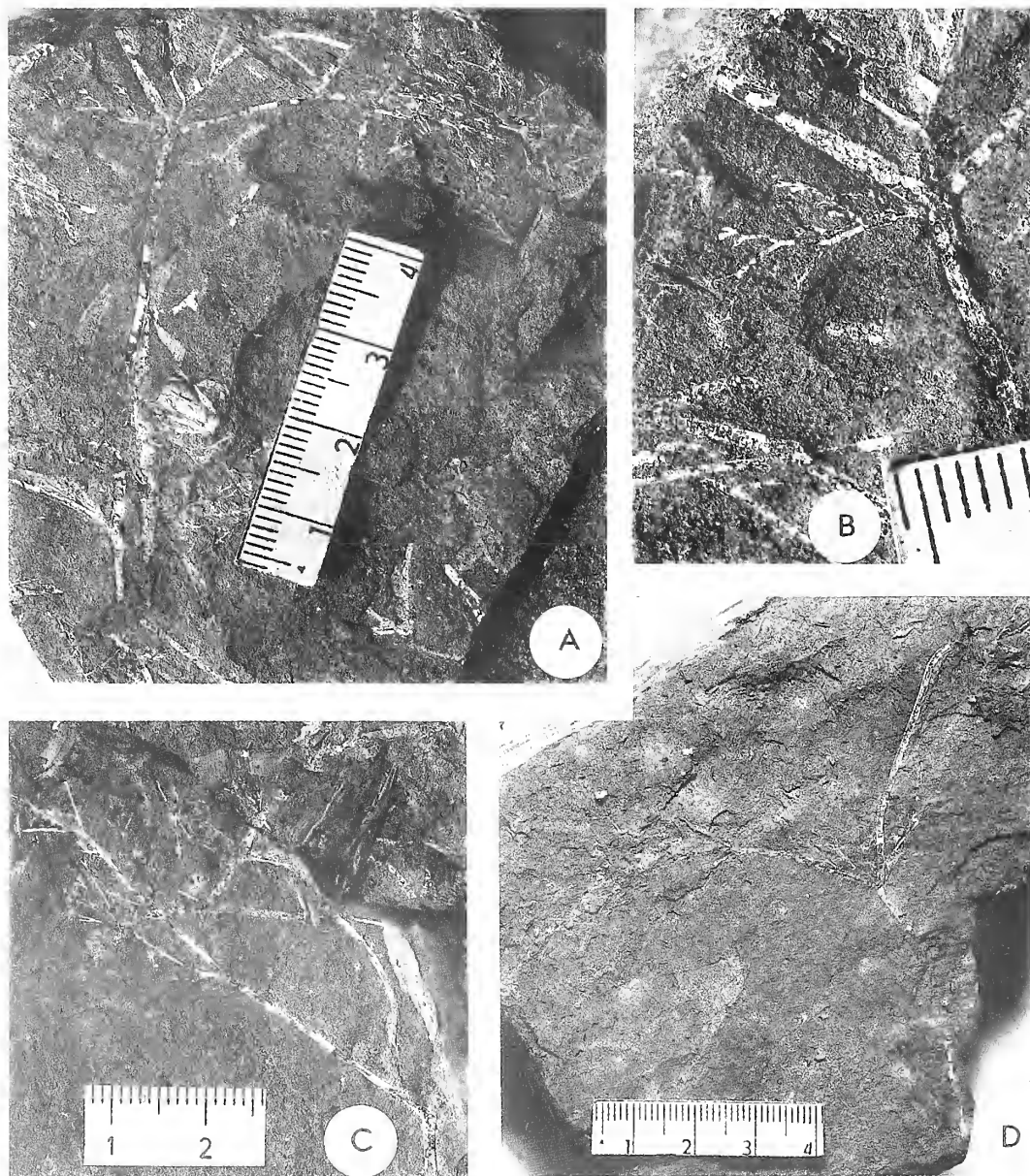


Fig. 38A-D. Probable progymnosperm: A. Axis with two unequal bifurcations alternately arranged; B. Detail of A showing fine axes terminating in expanded tips; C. Thinner branch arising from point of bifurcation; D. Axis showing unequal bifurcation.

unequivocally assigned to any particular algal or plant group at present. A selection of these is illustrated in Figs 39-41.

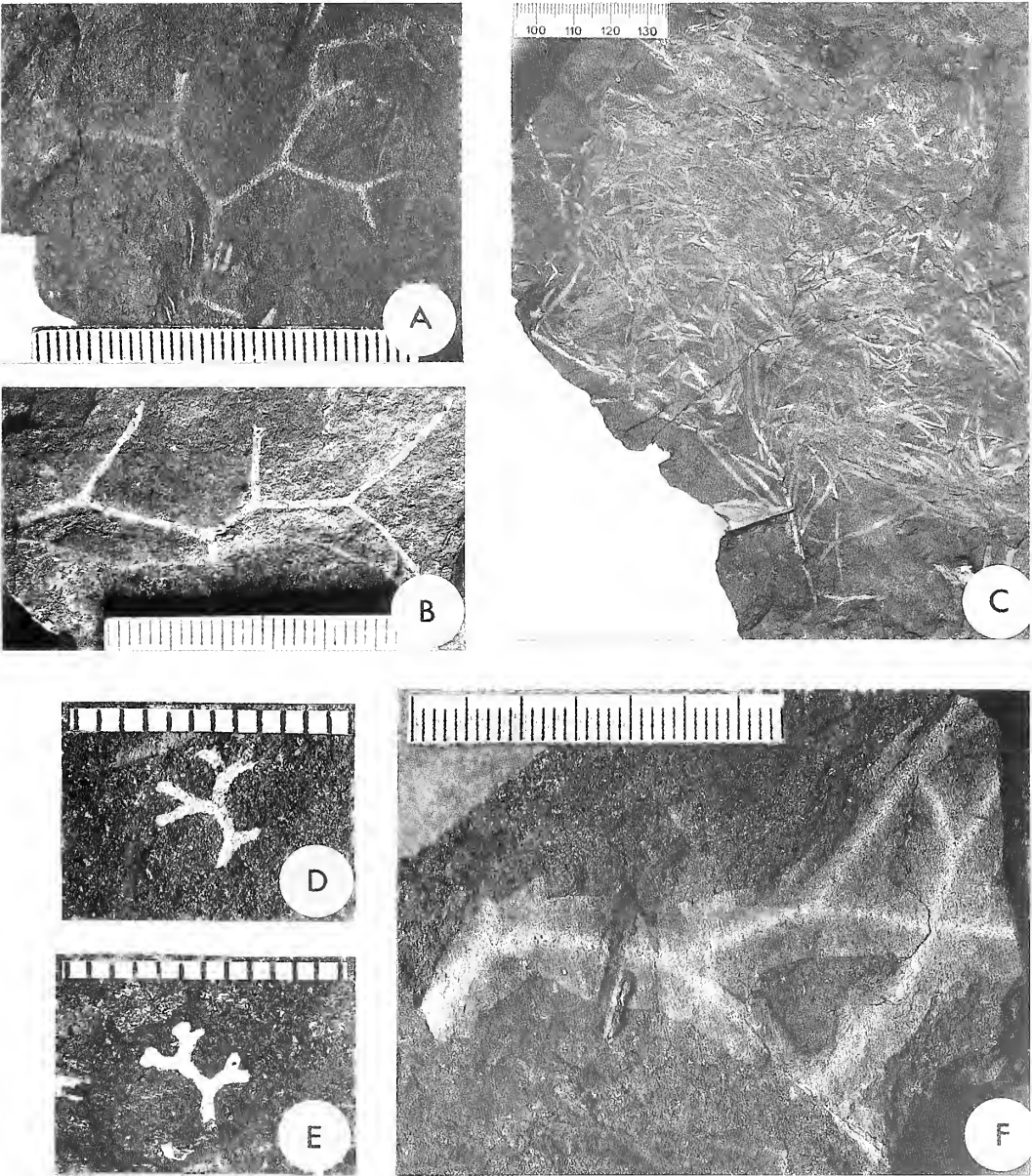


Fig. 39. Incertae sedis.

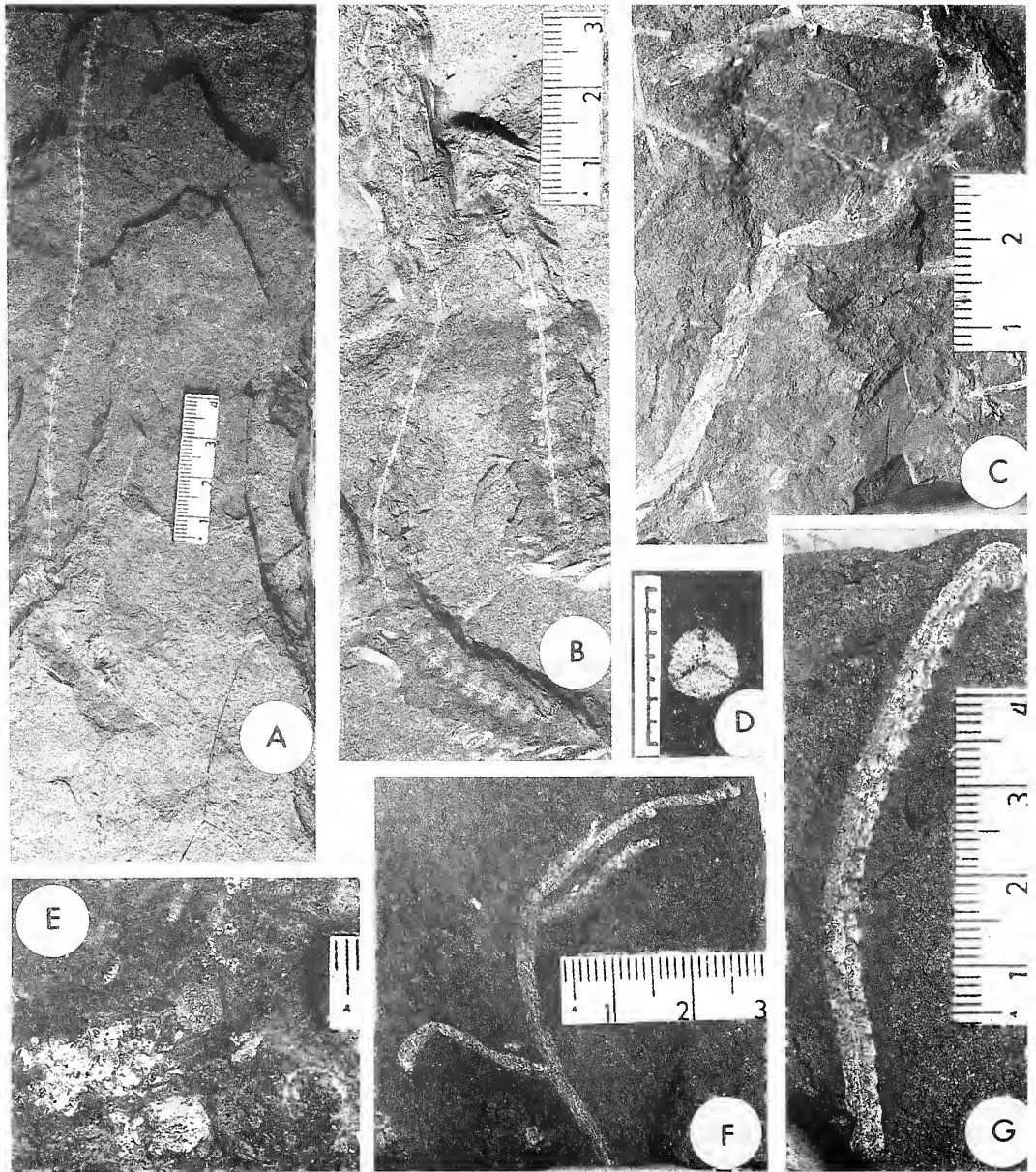


Fig. 40. Incertae sedis.

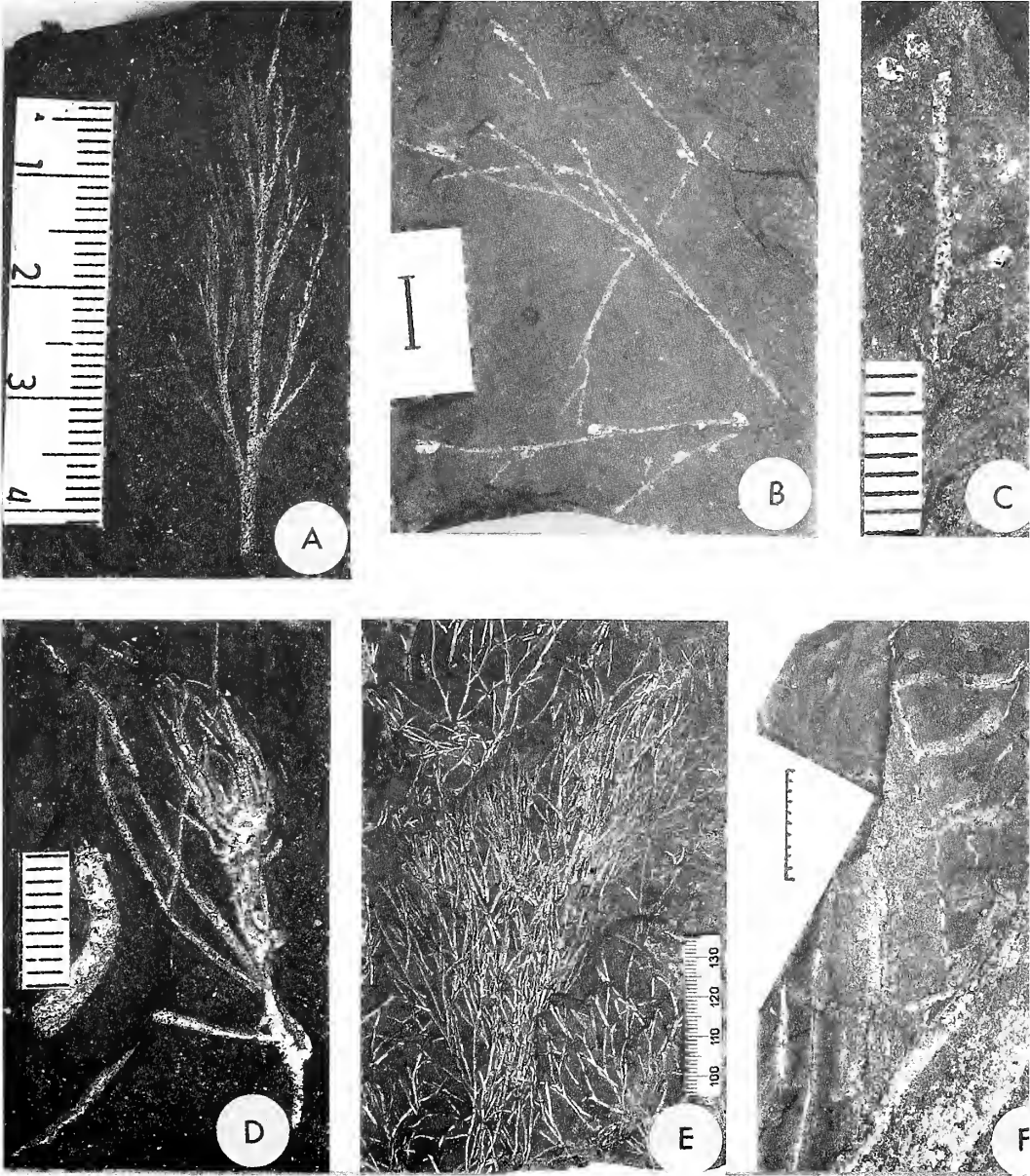


Fig. 41. Incertae sedis.

ANIMALS

Arthropoda (Figs 42-44)

The largest arthropod remains that have been recovered consist of occasional fragments of eurypterid. The fragments were seemingly in a poor state prior to burial, perhaps reflecting the action of scavengers and/or the relatively thin exoskeleton of eurypterids. Specimens include a possible posterior limb (Fig. 42C), other limb fragments (Fig. 42D-E), a gnathostome (Fig. 42F), and several fragmentary remains of body segments (Figs 43A, B). The only previously-reported eurypterids from the Witteberg Group are *Hastimima* sp. from the Weltevrede Formation (Seward, 1909; Woodward, 1909) and *Cyrtoctenus wittebergensis* Waterston *et al.*, 1985 from the Waaipoort Formation. Given the state of preservation, it is very difficult to say to which, if either, of these forms the present material belongs. The former comes from older strata while the latter was found in younger rocks and it may be that the new Witpoort Formation remains represent a different taxon.

Fairly common at the site, although often poorly preserved, are the remains of a large conchostracan (Fig. 43D-G), which reaches up to 15 mm in width and 25 mm in length. Very small specimens may represent a separate species. The material may belong to *Palaeostheria* sp., described by Rennie (1934), in association with plant fragments including *Haplostigma*, from the somewhat older black shale at Port Alfred. The type material of this species is, however, not well enough preserved to allow thorough comparison.

Several species of ostracod have also been found. Most of the specimens have unornamented carapaces (Fig. 44) but a single much smaller specimen, a mere 0.8 mm long, displays an interestingly sculptured shell with two protrusions on each valve, a short distance from the hinge line (Fig. 43C).

Pisces

Fish material from the Grahamstown site can be assigned to several groups including acanthodians, placoderms, chondrichthyans, crossopterygians, and dipnoans (Anderson *et al.*, 1994). Of these, the placoderms are the most common.

A series of more in depth plans on the fish material is to be prepared in conjunction with Dr J.A. Long and Dr M.E. Anderson.

Placoderms (Figs 45-55)

The placoderms are represented by arthrodires and antiarchs. The arthrodire material includes three main types, the most common of which (Figs 45C, 46-49) is known from small juveniles (Fig. 49A) to large adults (Fig. 48A-B), and is assignable to the genus *Groenlandaspis* (pers. comm. A. Ritchie, September 1993). It is characterised by an unusually high anterior lateral plate (Figs 47G, 48C,E, 49D). Most plates of this species have been found dissociated (Fig. 49B-D). Another possible *Groenlandaspis* (Figs 50A-B, E-G, I-J, 51) has a lower anterior lateral plate (Fig. 50E) and a longer, more tapering spinal plate (Figs 50A, B, I, 51D). A third groenlandaspidid arthrodire (Fig. 52A-D) that may belong to a different genus was recognised among our specimens by Dr J.A. Long (September 1994). It has an extremely high median dorsal plate (Fig. 52A-D) but is represented at present by only a few isolated plates.

Other arthrodire material (Fig. 45A,B) consisting of two plates bearing a distinctive ornament cannot at present be further identified.

The only antiarch as yet recovered belongs to the genus *Bothriolepis* and is well represented by both juvenile (Fig. 53) and large adult (Figs 54, 55A-D) specimens. This is probably a new species (pers. comm. J.A. Long, September 1994). As with the arthrodires, small individuals are fairly well articulated but the larger adult forms are mostly disarticulated.

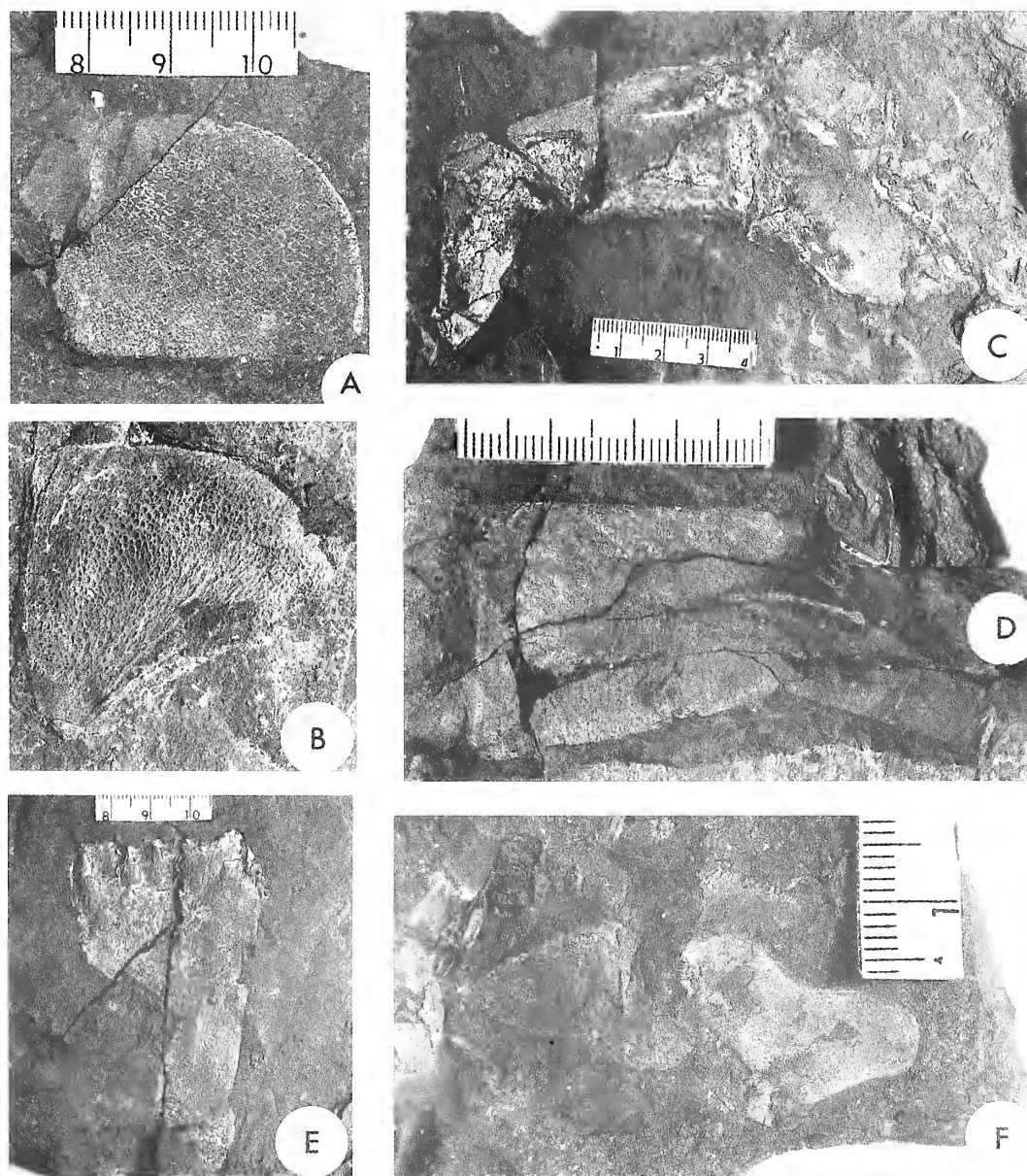


Fig. 42A-F. Eurypterida: A-B. Body parts (to same scale); C. Possible posterior limb, D. Limb fragment, E. Portion of limb, F. Gnathostome.

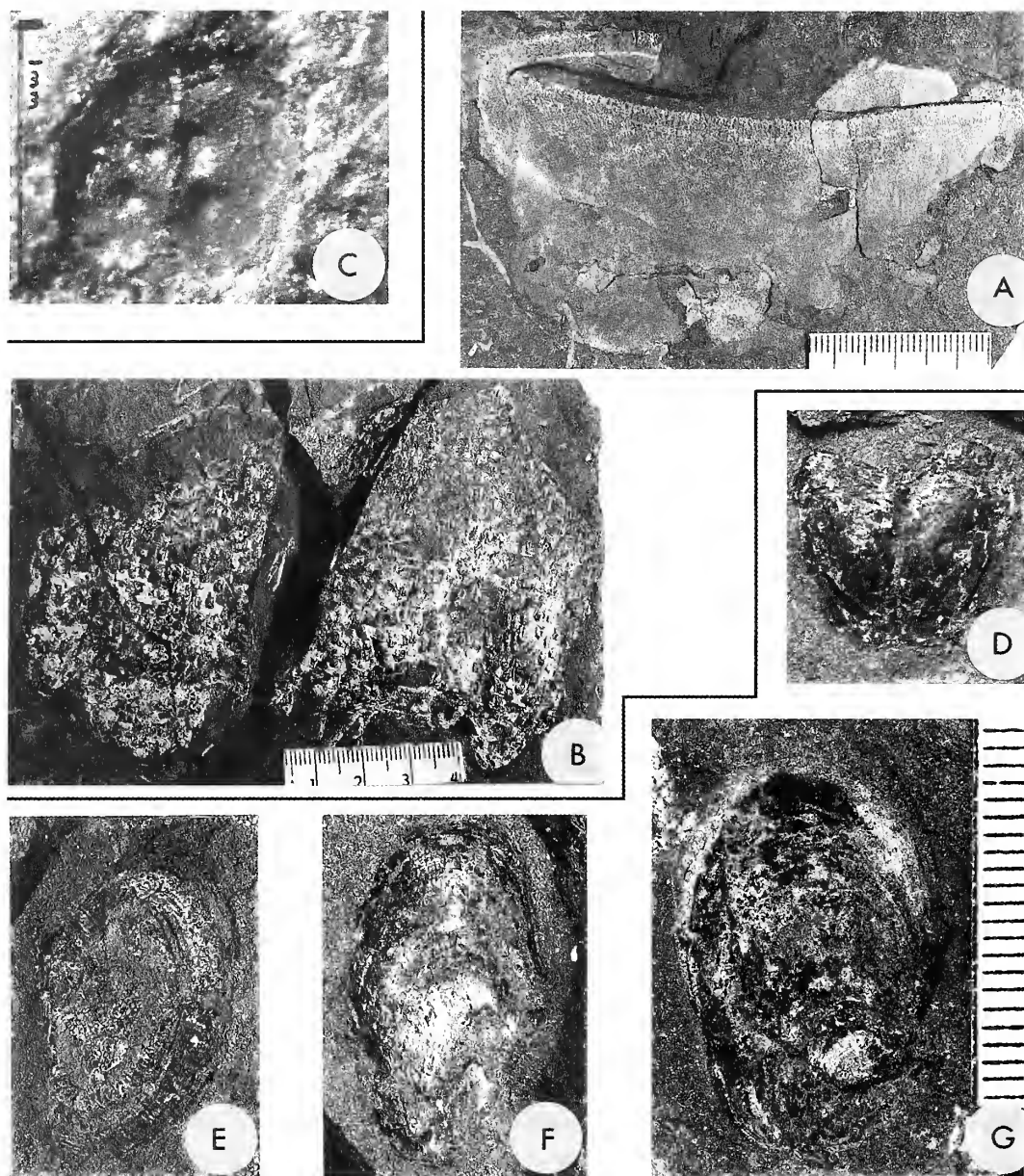


Fig. 43A-G: A-B. Pieces of eurypterid body segments; C. Ornamented ostracod; D-G. Conchostracans (? *Palaeoestheria* sp.) (to same scale).

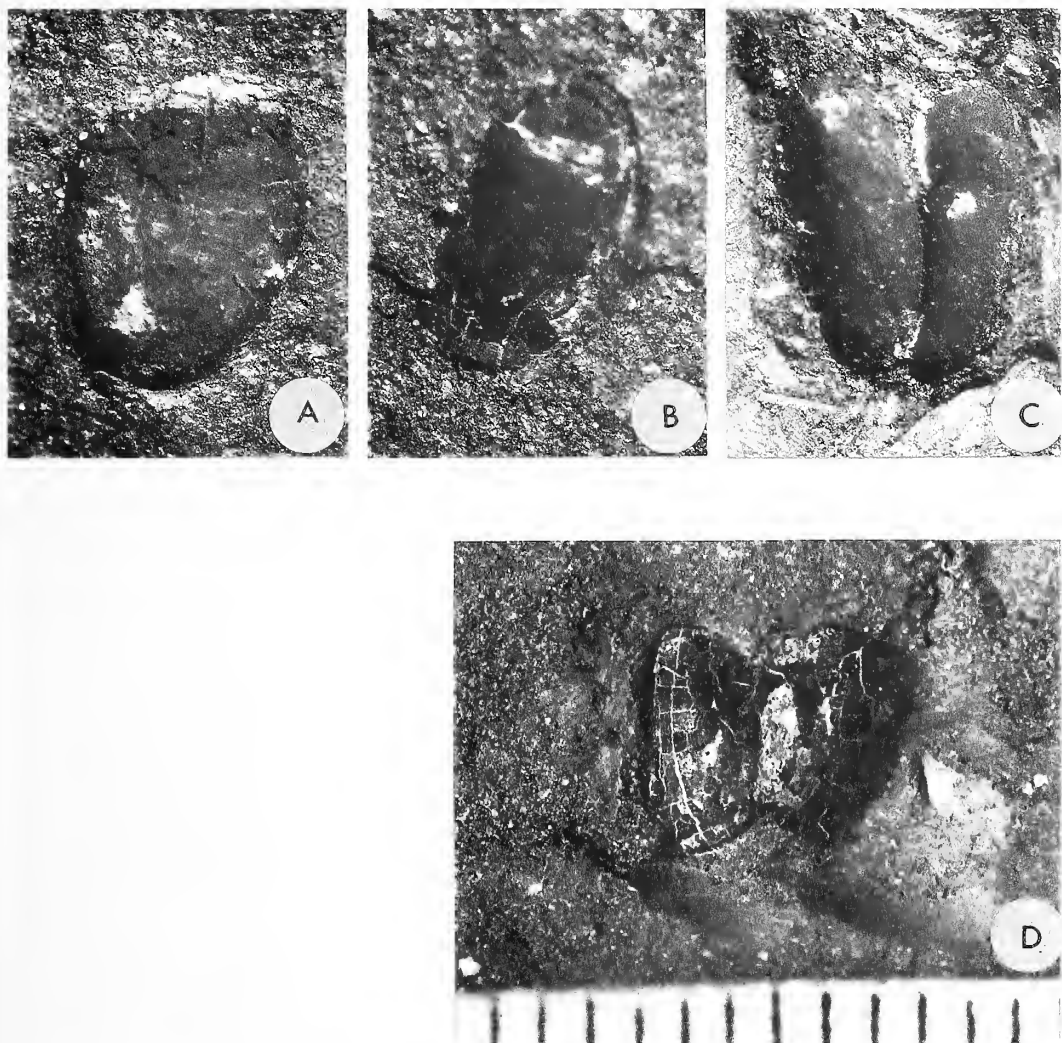


Fig. 44A-D. Various unornamented ostracods (A. 1.83mm long, B. 2.08mm long, C. 1.83mm long).

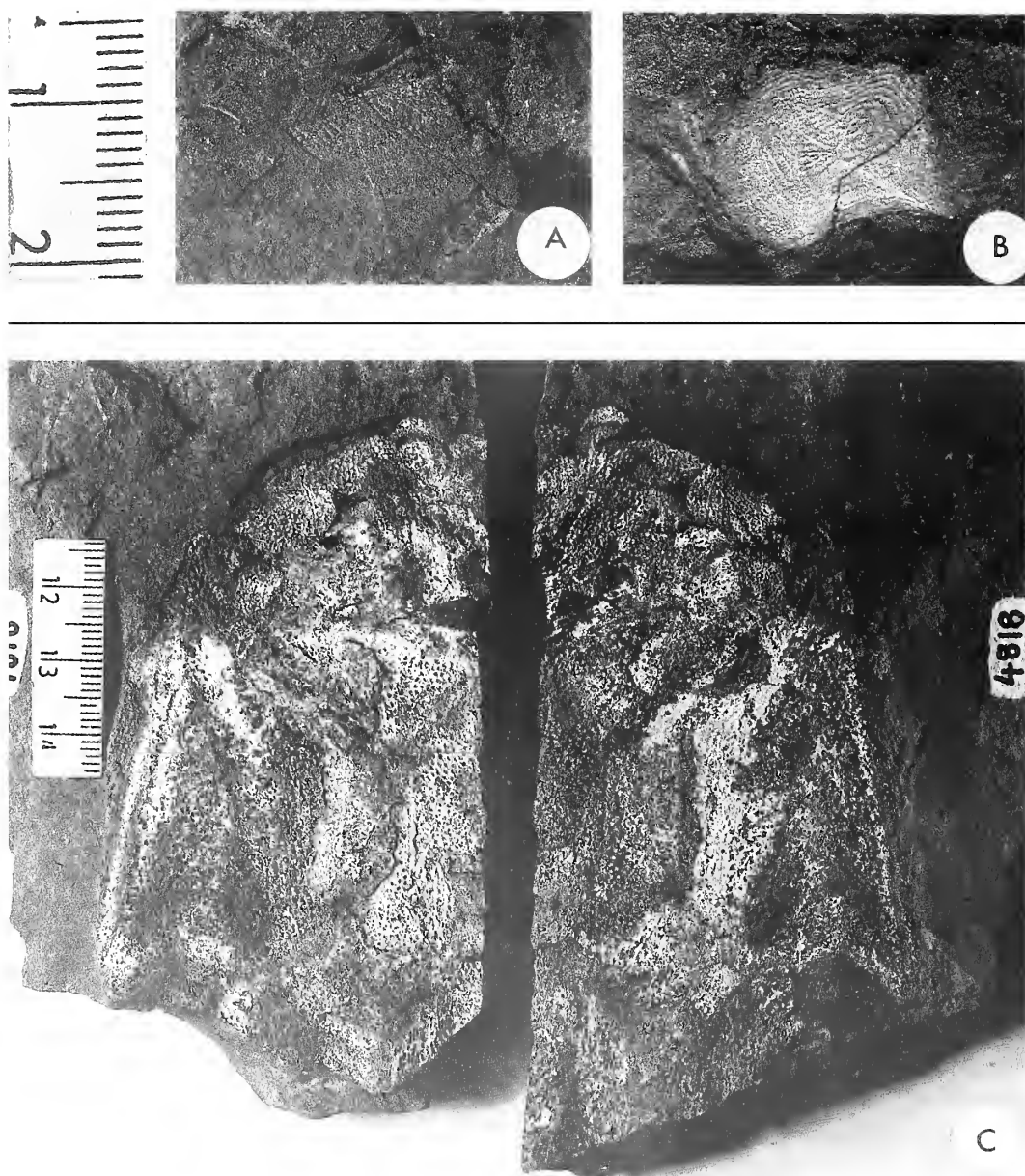


Fig. 45A-C. Arthrodire placoderm fish remains: B. Possible Anterior Ventrolateral plate; C. Articulated *Groenlandaspis* sp. head and trunk plates (pers. comm. John Long, September 1994).

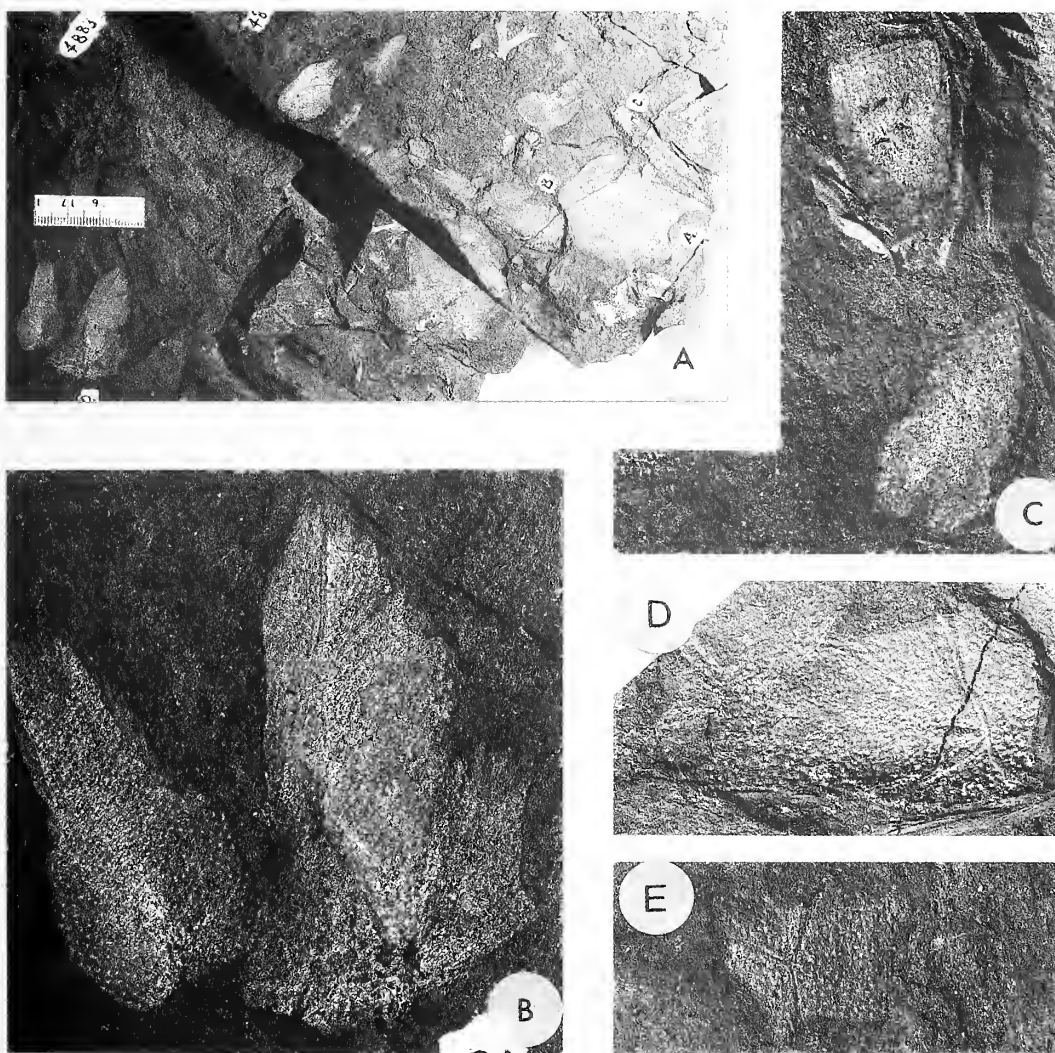


Fig. 46 A-E. *Groenlandaspis* sp.: A. Dissociated *Groenlandaspis* sp. head and trunk plates, Anterior Ventrolateral (trunk) plate at bottom right; B-E. Details of specimen in A (to scale): B. Nuchal at left, right Paranuchal at bottom right, right Central at top right (head plates), C. Pineal (head) plate at bottom, D. Suborbital (head) plate, E. Postorbital (head) plate.

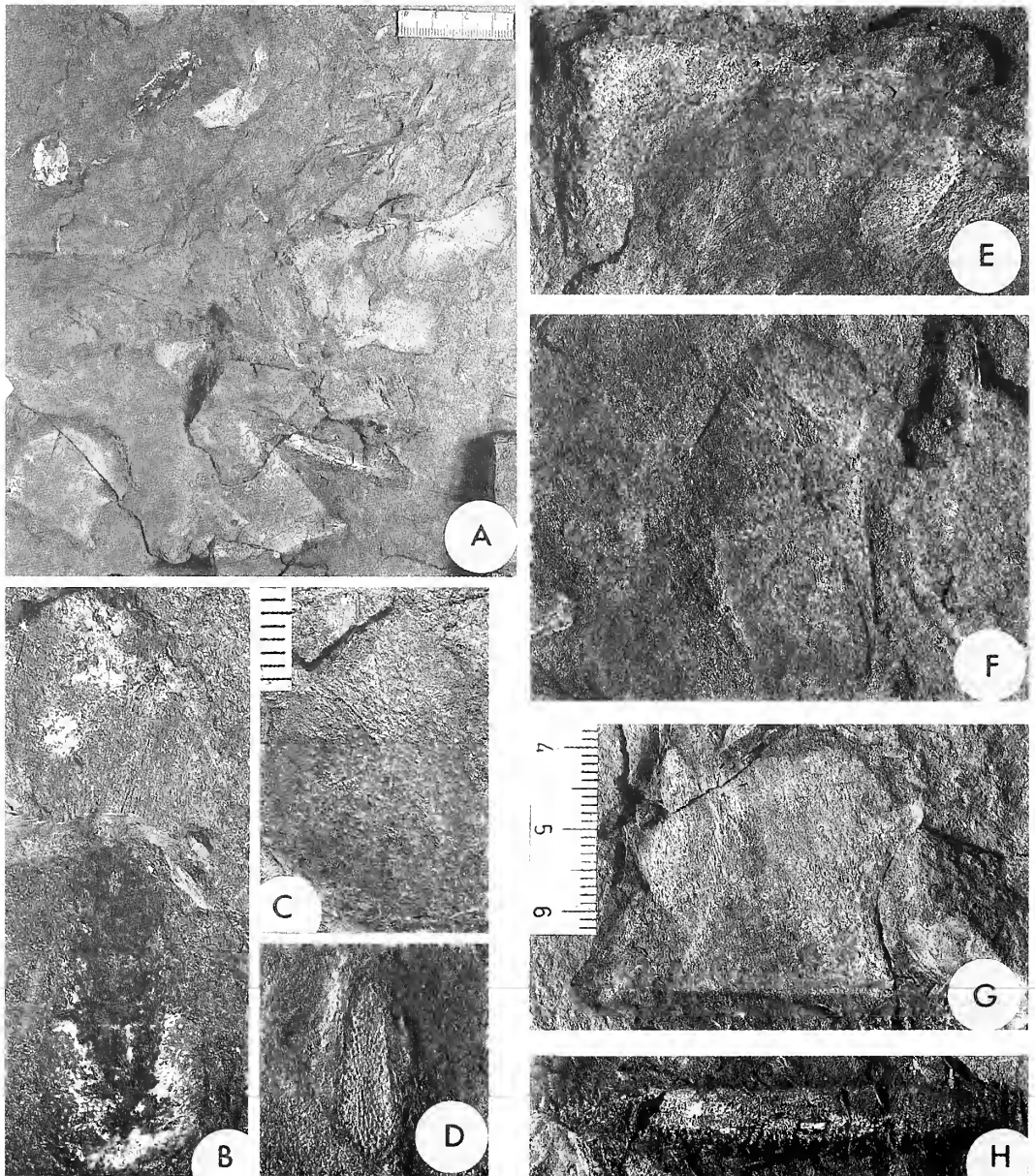


Fig. 47 A-H. *Groenlandaspis* sp. : A. Dissociated *Groenlandaspis* sp. head and trunk plates (B-D to scale, E-H to scale); B-H. Details of specimen in A. B. Paranuchal (head) plate at top, Nuchal (head) plate at bottom, C. Central (head) plate, D. Possible superagnathal bone, E. Median Dorsal (trunk) plate, F. Posterior Dorsolateral (trunk) plate, G. Anterior Dorsolateral (trunk) plate, H. Spinal plate.

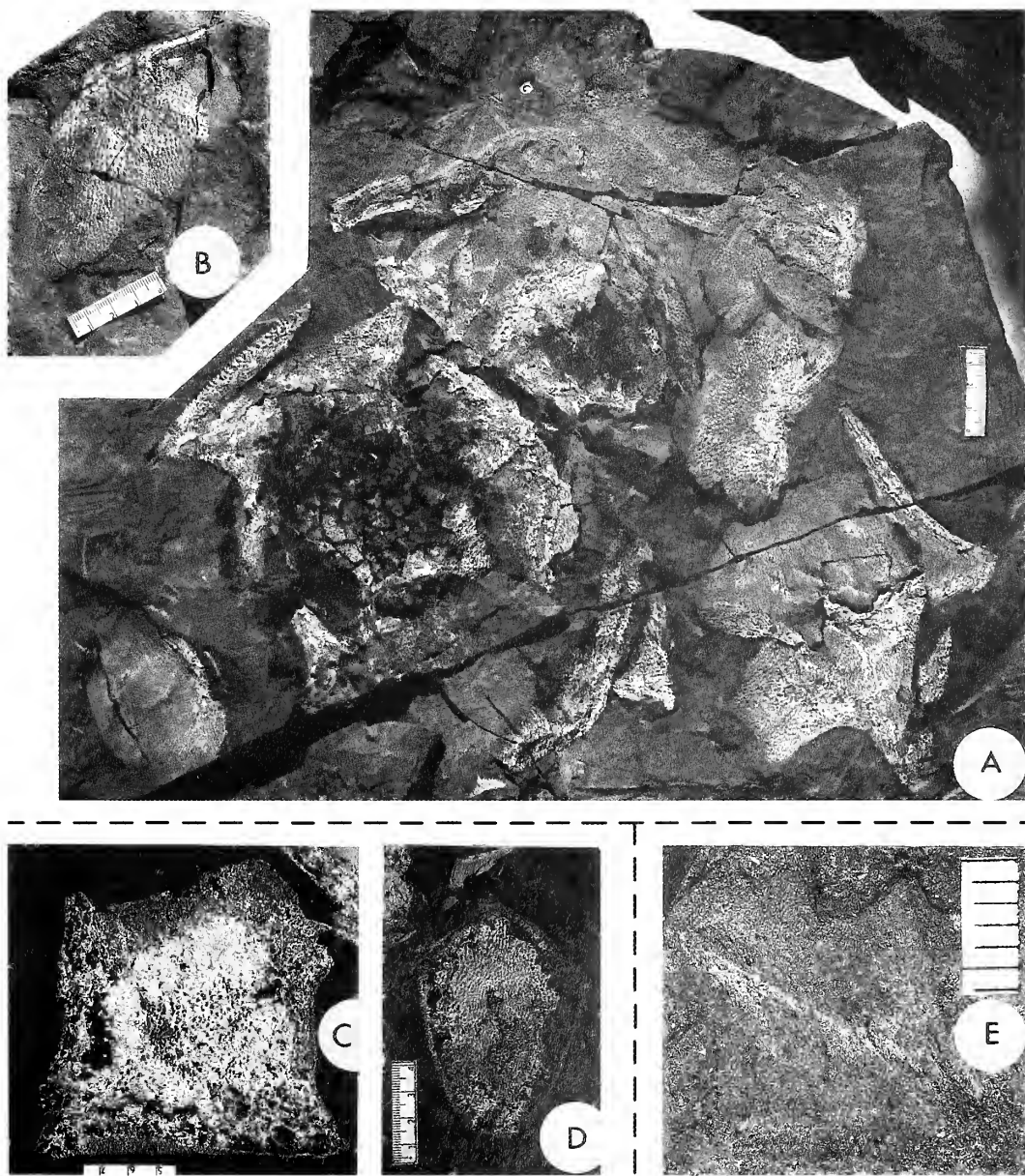


Fig. 48A-E. *Groenlandaspis* sp.: A. Semiarticulated head and trunk plates; head at top; B. Anterior Dorsolateral (trunk) plate of specimen in A (most anterior ventral point at top right); C-D. Anterior Lateral, and Posterior Median Ventral (trunk) plates of largest specimen found; E. Anterior Lateral (trunk) plate of small individual.

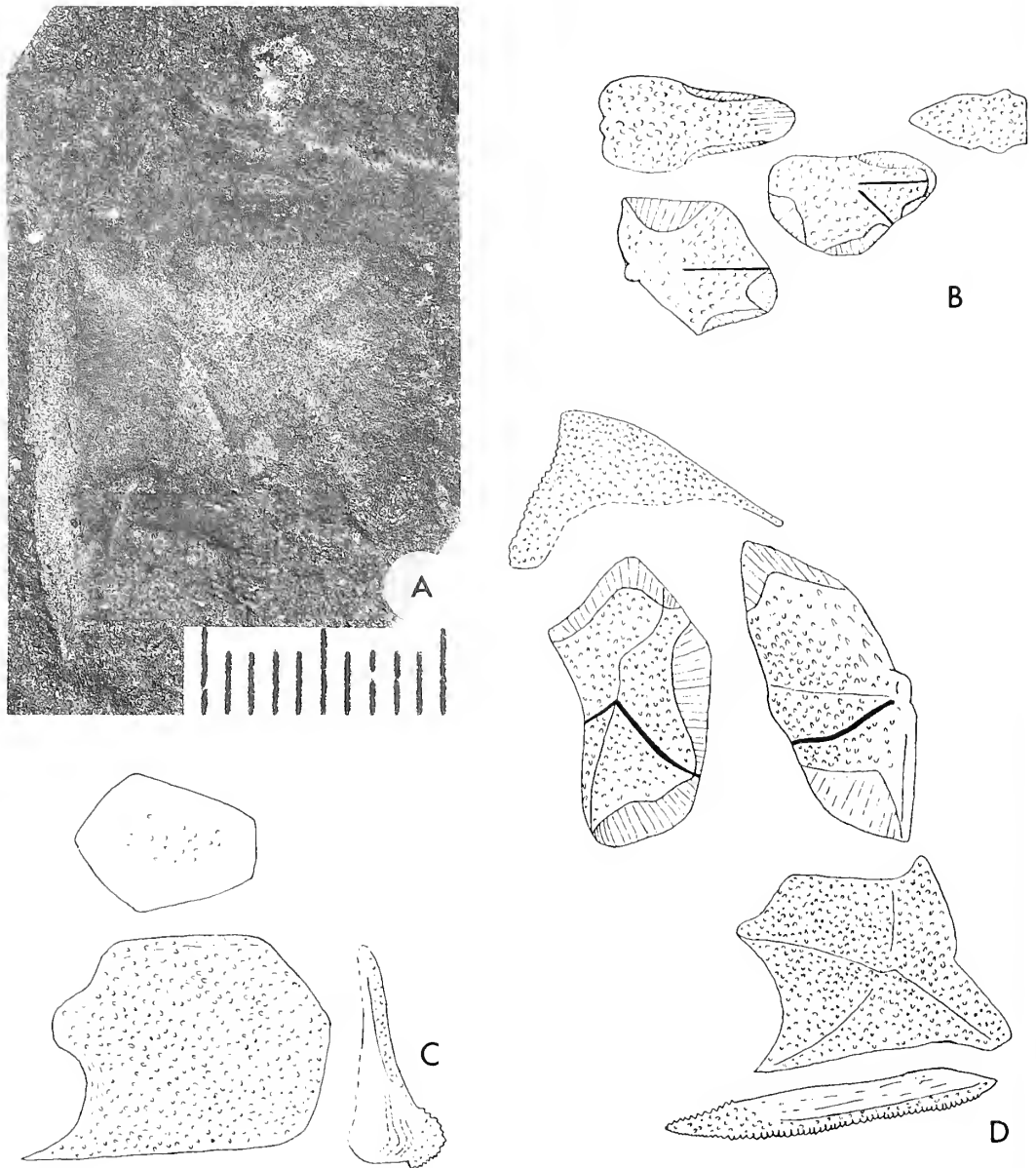


Fig. 49A-D. *Groenlandaspis* sp.: A. Partially articulated juvenile left trunk; B. Preliminary reconstruction of right central head shield plates, clockwise from top left - Nuchal plate, Pineal plate, Central plate and Parannuchal plate; C. Preliminary reconstruction of ventral trunk plates, clockwise from top - Posterior Median Ventral plate, left Interolateral plate, left Anterior Ventrolateral plate; D. Preliminary reconstruction of right dorsolateral trunk plates, clockwise from top - Median Dorsal plate, Anterior Dorsolateral plate, Spinal plate and Posterior Dorsolateral plate. (B-D as in Anderson *et al.* 1994).

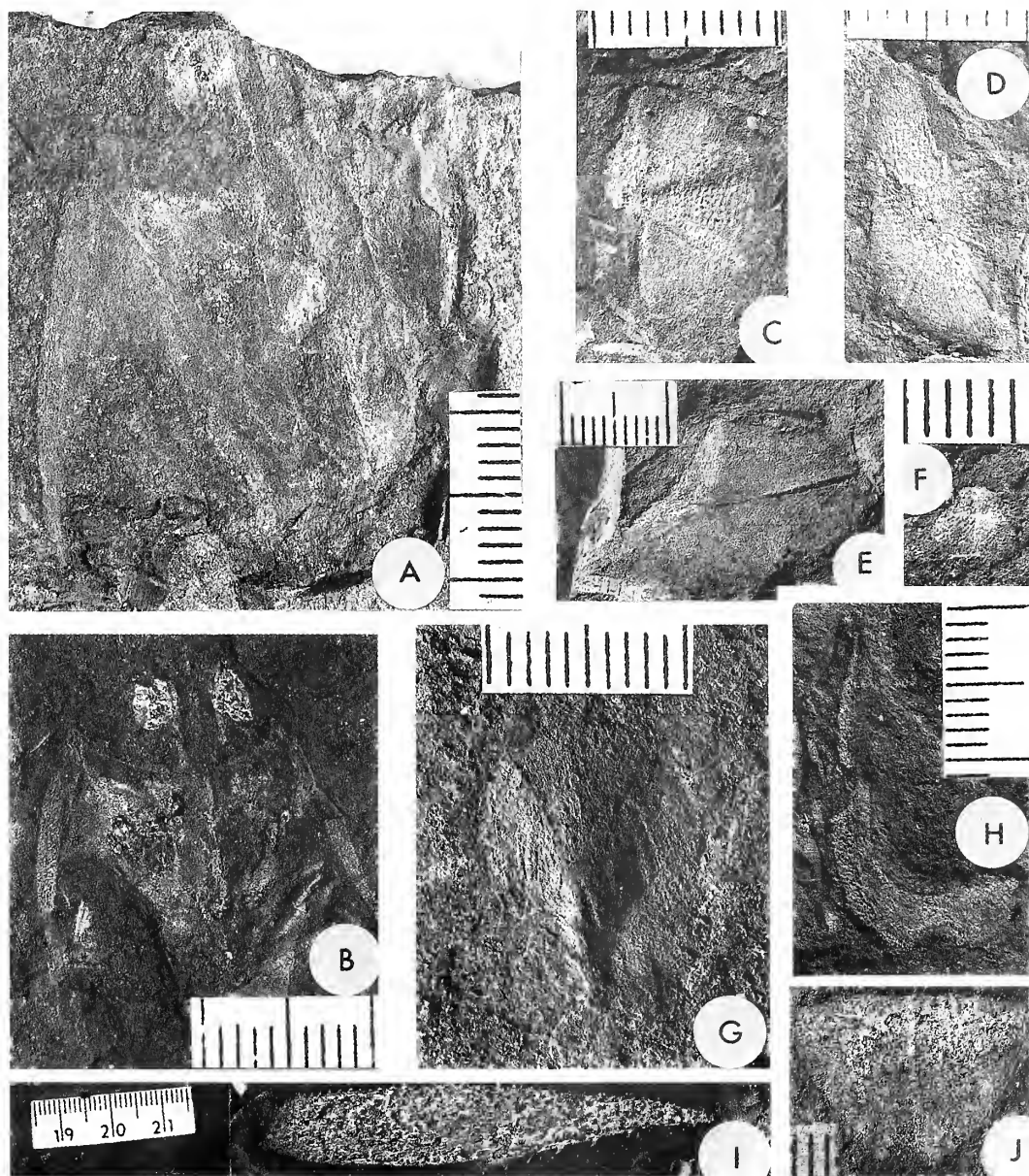


Fig. 50A-J: A-B. Head and trunk plates of small articulated type two groenlandaspids; C. Groenlandaspid Anterior Dorsolateral (trunk) plate; D. ? Type three groenlandaspid Posterior Dorsolateral (trunk) plate; E. Type two groenlandaspid Anterior Lateral (trunk) plate; F. Type two groenlandaspid plate; G. Type two groenlandaspid ? Median Dorsal (trunk) plate; H. Groenlandaspid trunk plate; I. Type two groenlandaspid Spinal (trunk) plate; J. Type two groenlandaspid ? Rostral (head) plate.

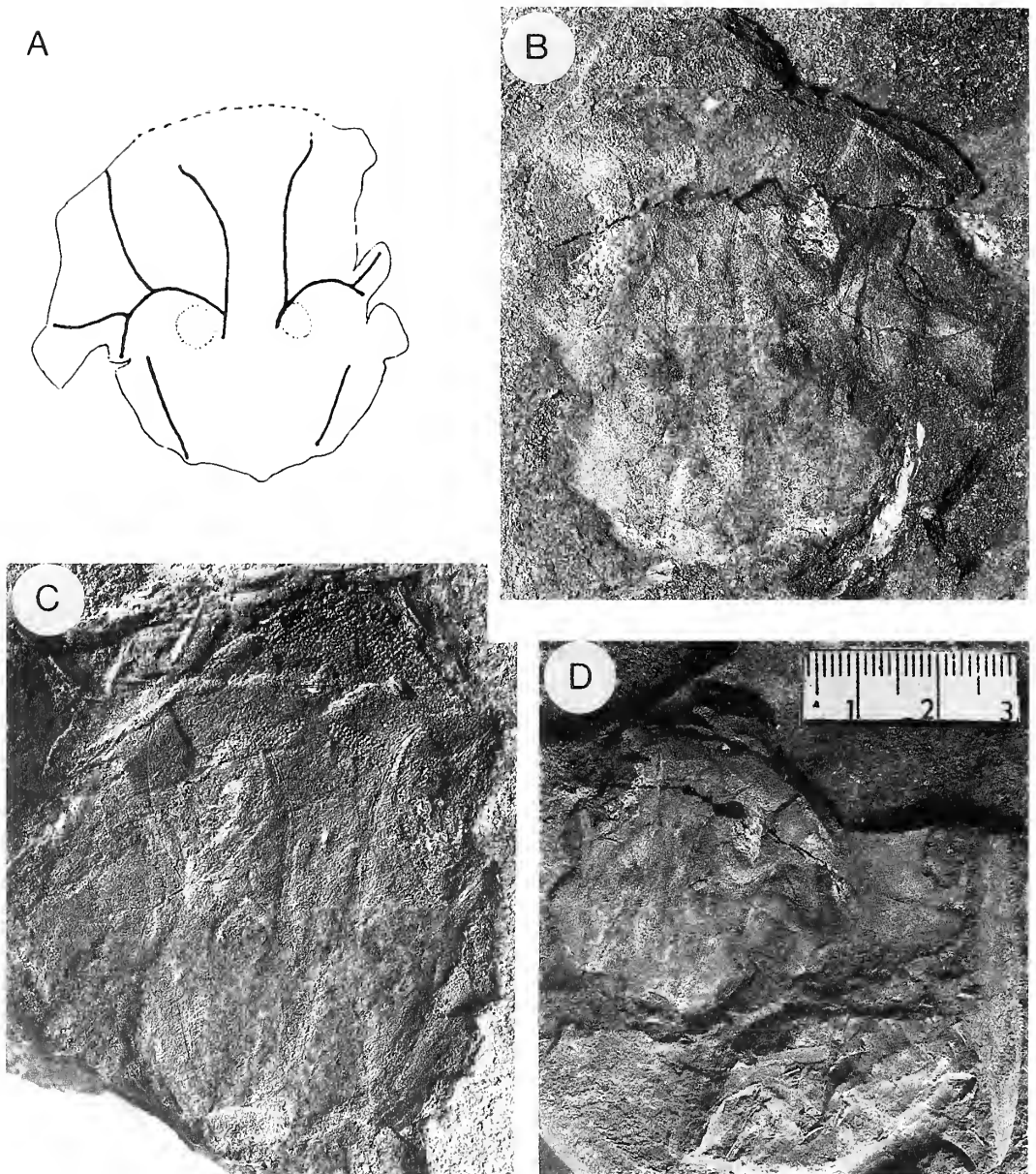


Fig. 51A-D. Specimen of type two groenlandaspidid: A. Line drawing of head shield showing canals (Median Dorsal (trunk) plate obscuring anterior margin); B-C. Specimen and counter specimen of head (Median Dorsal plate obscuring anterior in C); D. Head, Anterior Lateral (trunk) plate, and Spinal (trunk) plate.

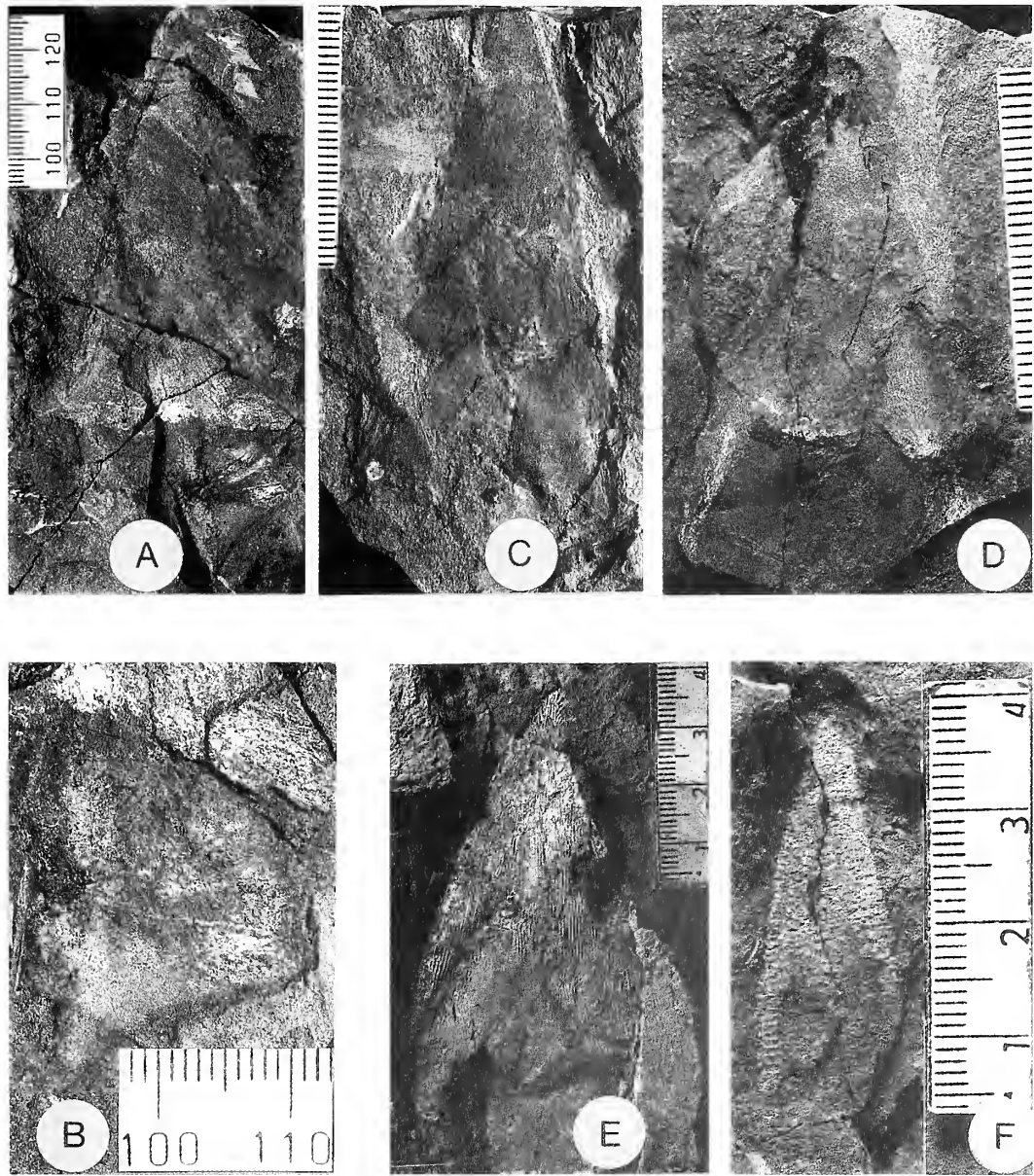


Fig. 52A-F. A. High Median Dorsal (trunk) plate with associated Anterior Dorsolateral (trunk) plate (right) of type three groenlandaspisid; B. Detail of Anterior Dorsolateral plate in A; C. Semi-articulated type three groenlandaspisid trunk plates. Median Dorsal plate (top), Anterior Dorsolateral plate (bottom right), Posterior Dorsolateral plate (bottom left); D. Counter specimen to specimen in C; E-F. Possible other high groenlandaspisid Median Dorsal (trunk) plates.

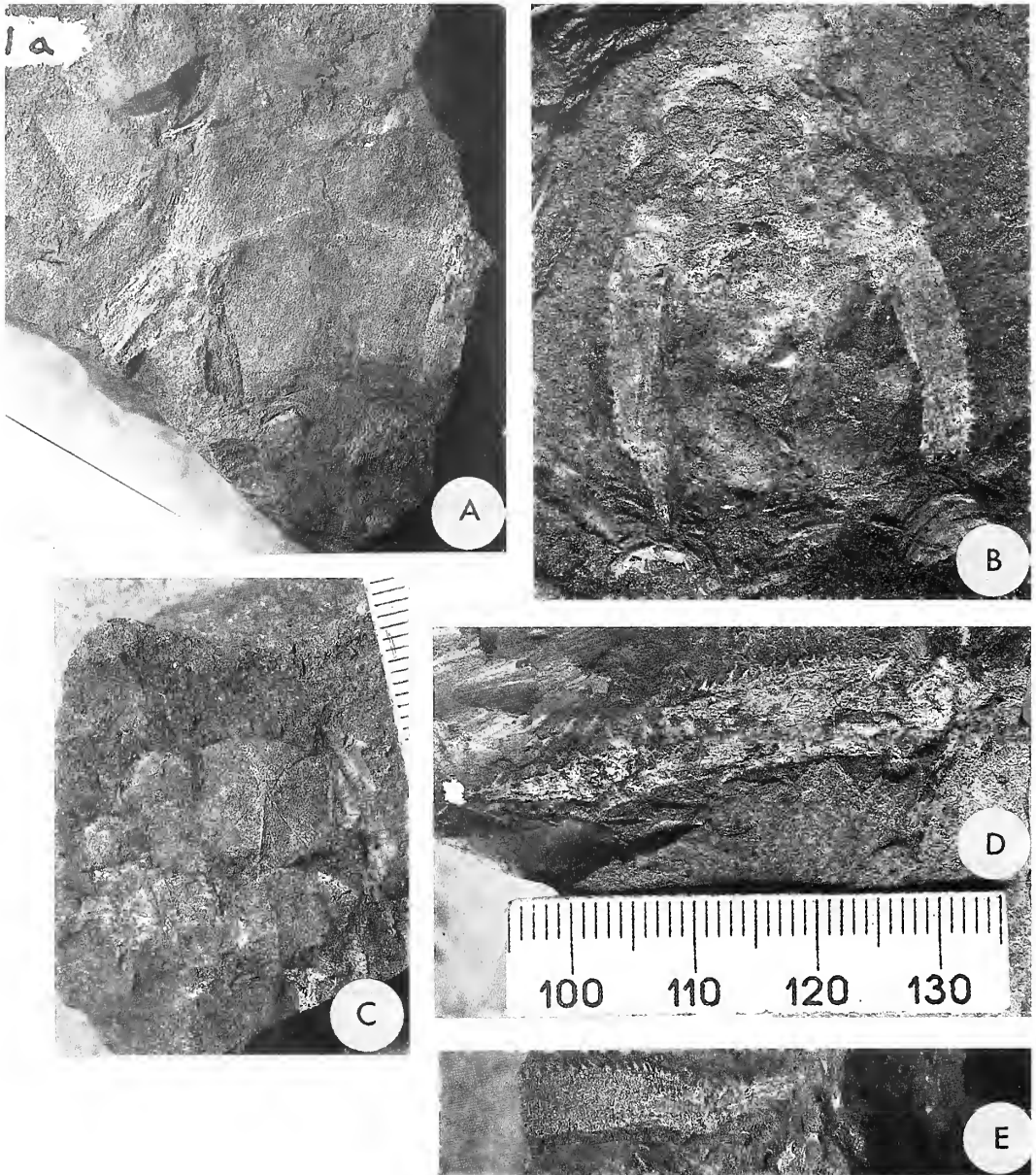


Fig. 53A-E. *Bothriolepis* sp. juveniles: A. Articulated ventral trunk plates; B. Specimen with both pectoral appendages; C. Part of dorsal trunk, Anterior Dorsolateral plate (top left), Anterior Median Dorsal plate (top centre), Posterior Median Dorsal plate (bottom centre); D-E. Pectoral appendages.

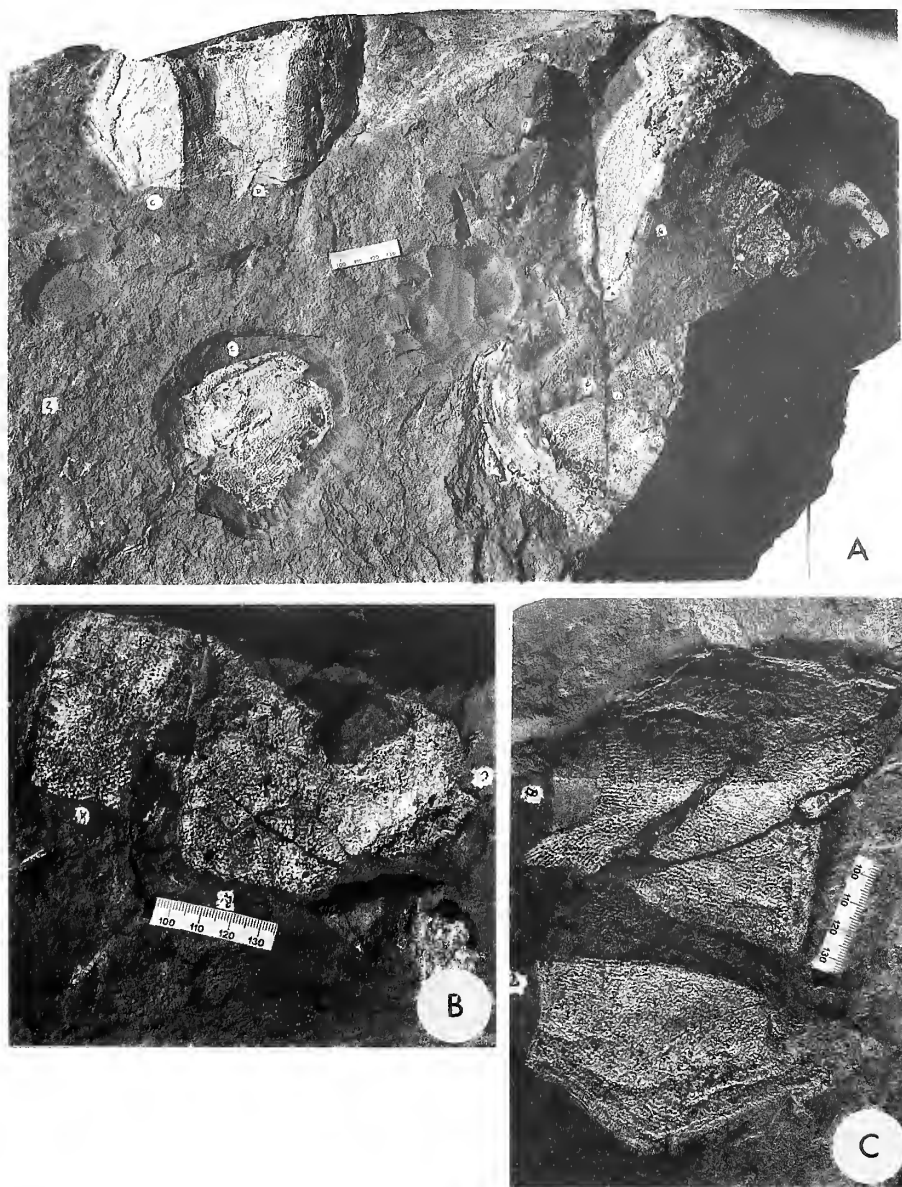


Fig. 54A-C. *Bothriolepis* sp., assemblage of adult plates: A. Anterior Dorsolateral (trunk) plate (top left), Mixilateral (trunk) plate (top centre), upper pectoral appendage (top right), Posterior Median Ventral (trunk) plate (centre); B. Near complete head, (piece of trunk at top left); C. Counter specimen of Mixilateral (top) and Anterior Dorsolateral (trunk) plates.

Acanthodians (Fig. 56)

The acanthodian material in our collection comprises a single isolated spine (Fig. 56E) and an

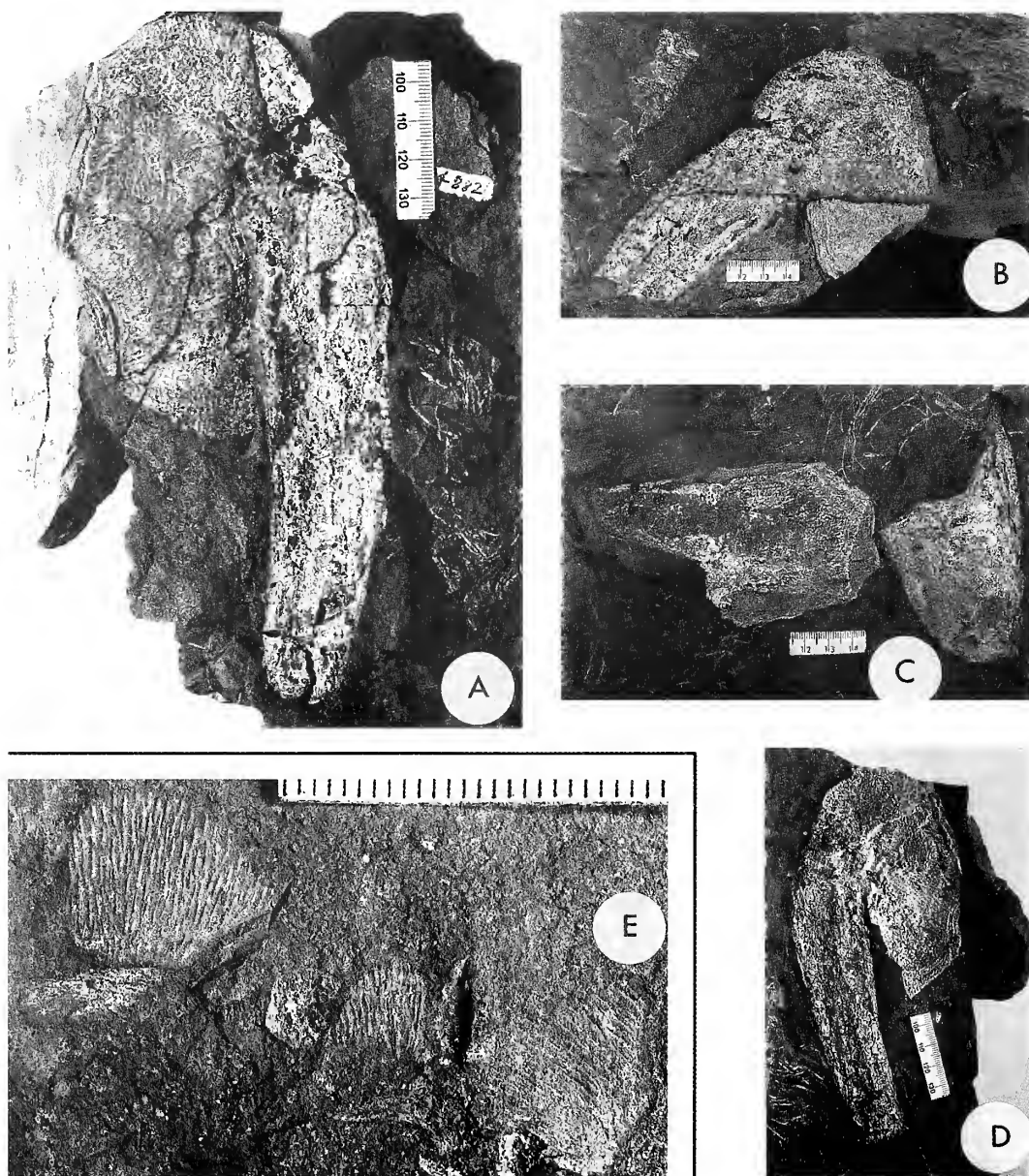


Fig. 55A-E: A-D. *Bothriolepis* sp. adult trunk plates: A-B. Pectoral appendages attached to Anterior Ventrolateral plates; C. Posterior Ventrolateral plate (at left); D. Counter specimen of A; E. Indeterminate piscean body scales.

assemblage of about 12 closely associated spines (Fig. 56A-D). The assemblage includes left and right spines and may well be derived from a single individual, possibly belonging to the Gyracanthidae (Anderson *et al.*, 1994).

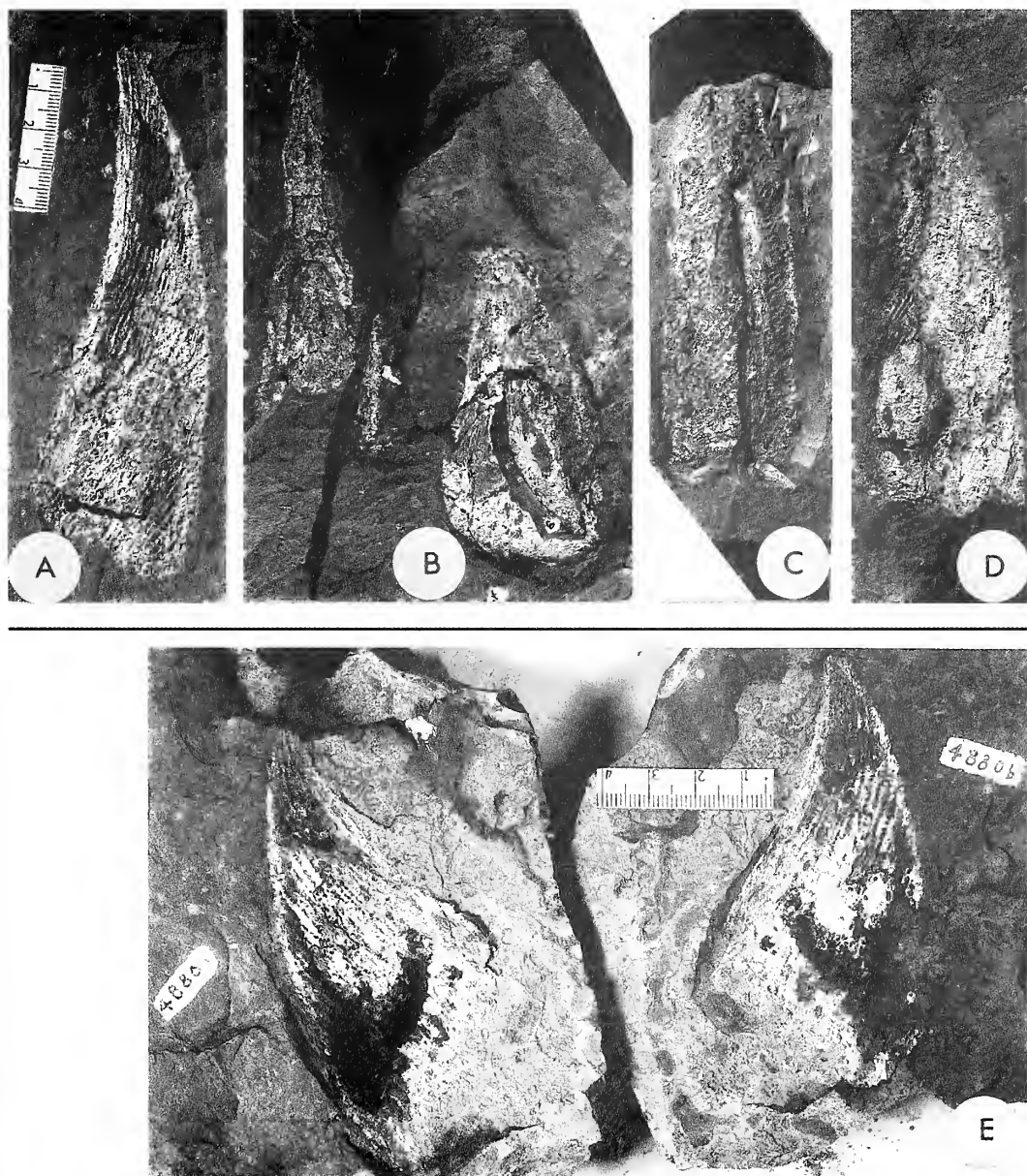


Fig. 56A-E: Acanthodian spines: A-D. Part of assemblage of twelve spines (to scale); E. Isolated spine with counter specimen.

Chondrichthyans (Figs 57,58)

Several specimens attributable to this group of fishes have been found at the Grahamstown site.

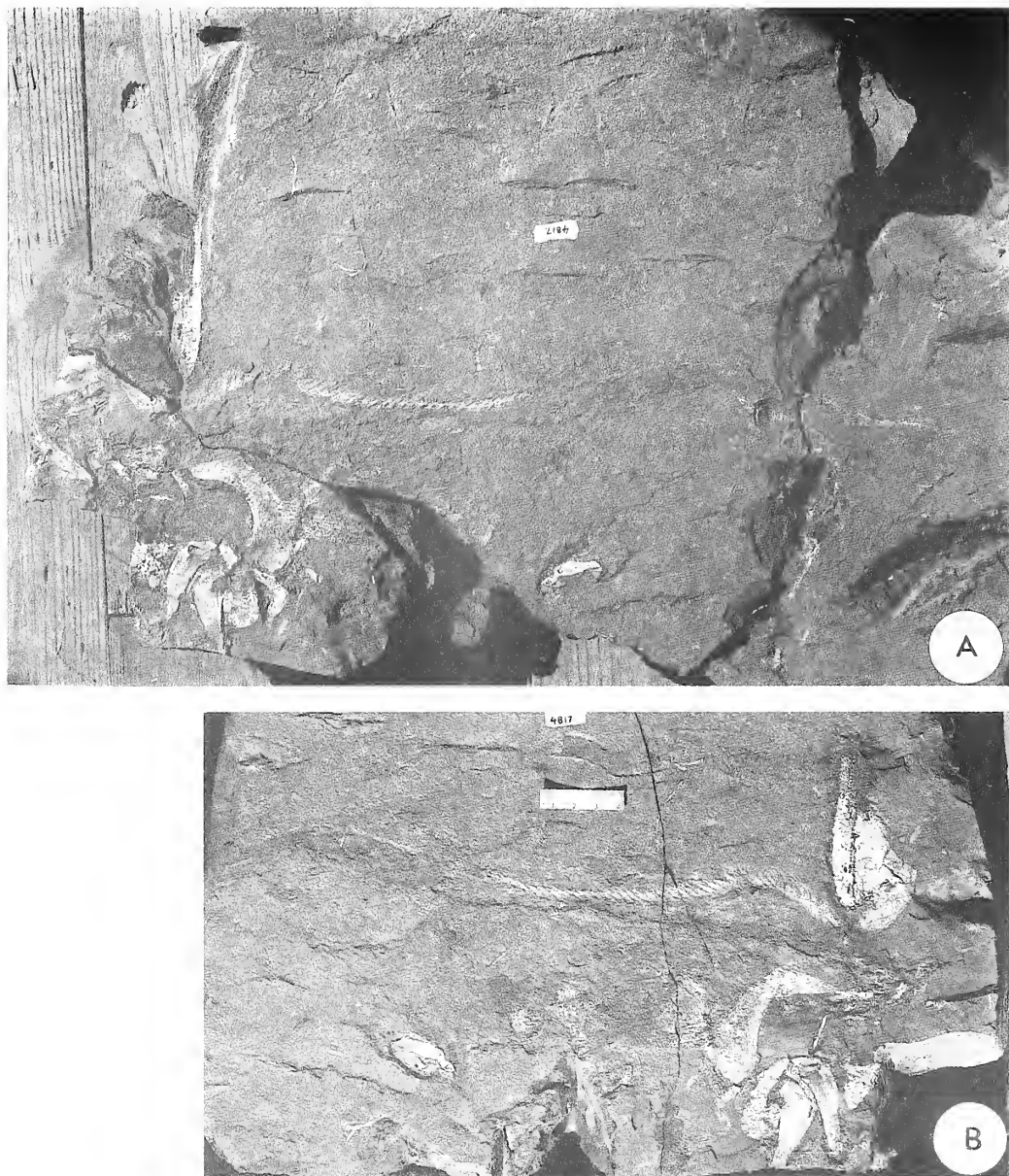


Fig. 57A and B: A. Whole bodied paraselachiomorph specimen showing (at left, top to bottom) high dorsal fin spine, spinal column (extending right), scapulocoracoid with attached pectoral fin, and displaced toothless lower jaws. A partial caudal fin impression is visible at the far right; B. Counter specimen to specimen in A, in which an apparent synsacral is visible at the base of the dorsal fin spine.

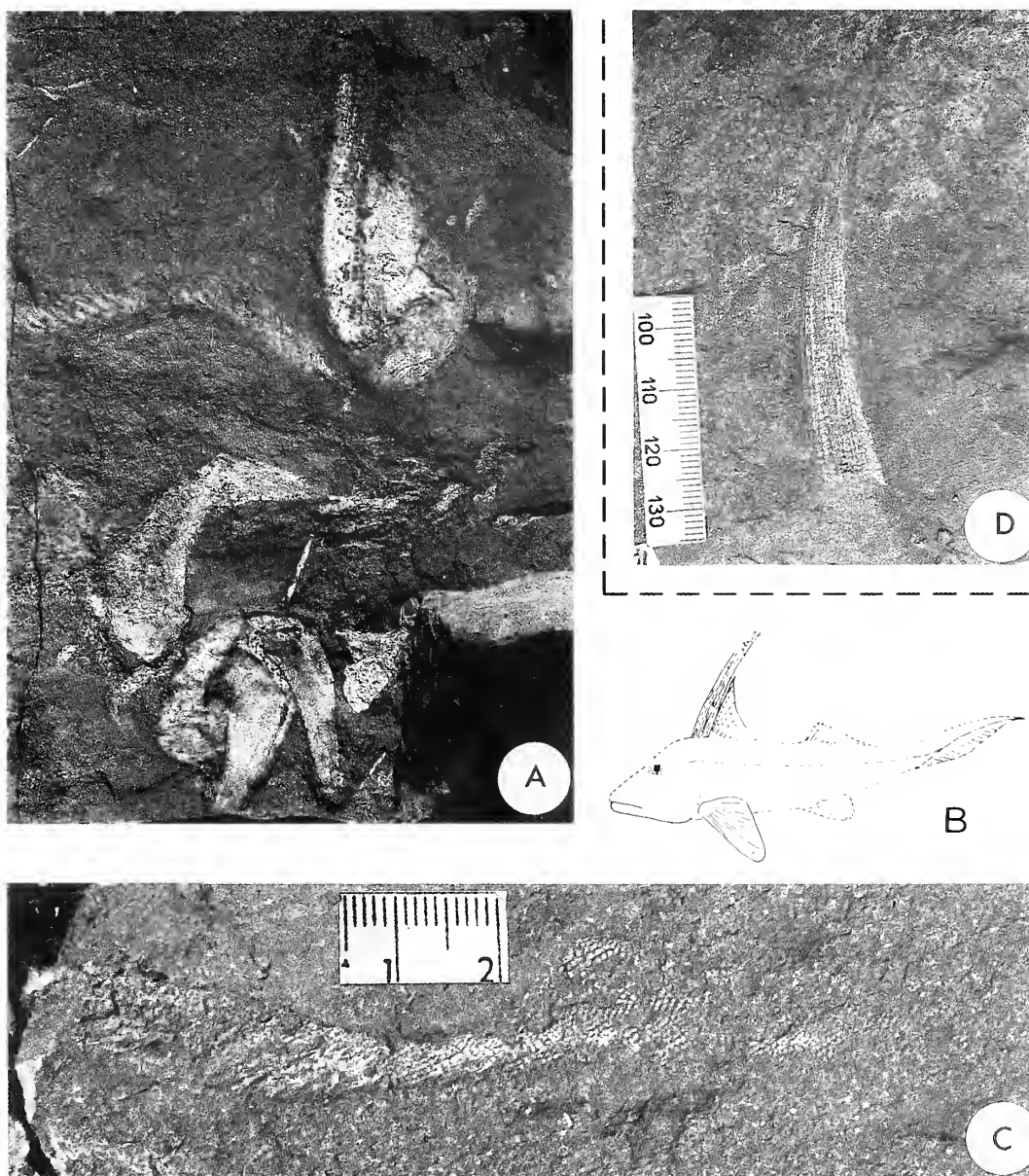


Fig. 58A-D: A. Enlargement of anterior of specimen in Fig. 57B; B. Possible reconstruction of the parselachiomorph; C. Enlargement of tail denticles of specimen in Fig. 57A; D. Dorsal fin spine of another individual with partial fin impression.

Three of these belong to a single previously unknown species. One specimen consists of a long dorsal spine with associated fin impressions (Fig. 58D), a second consists of an isolated lower jaw, and the

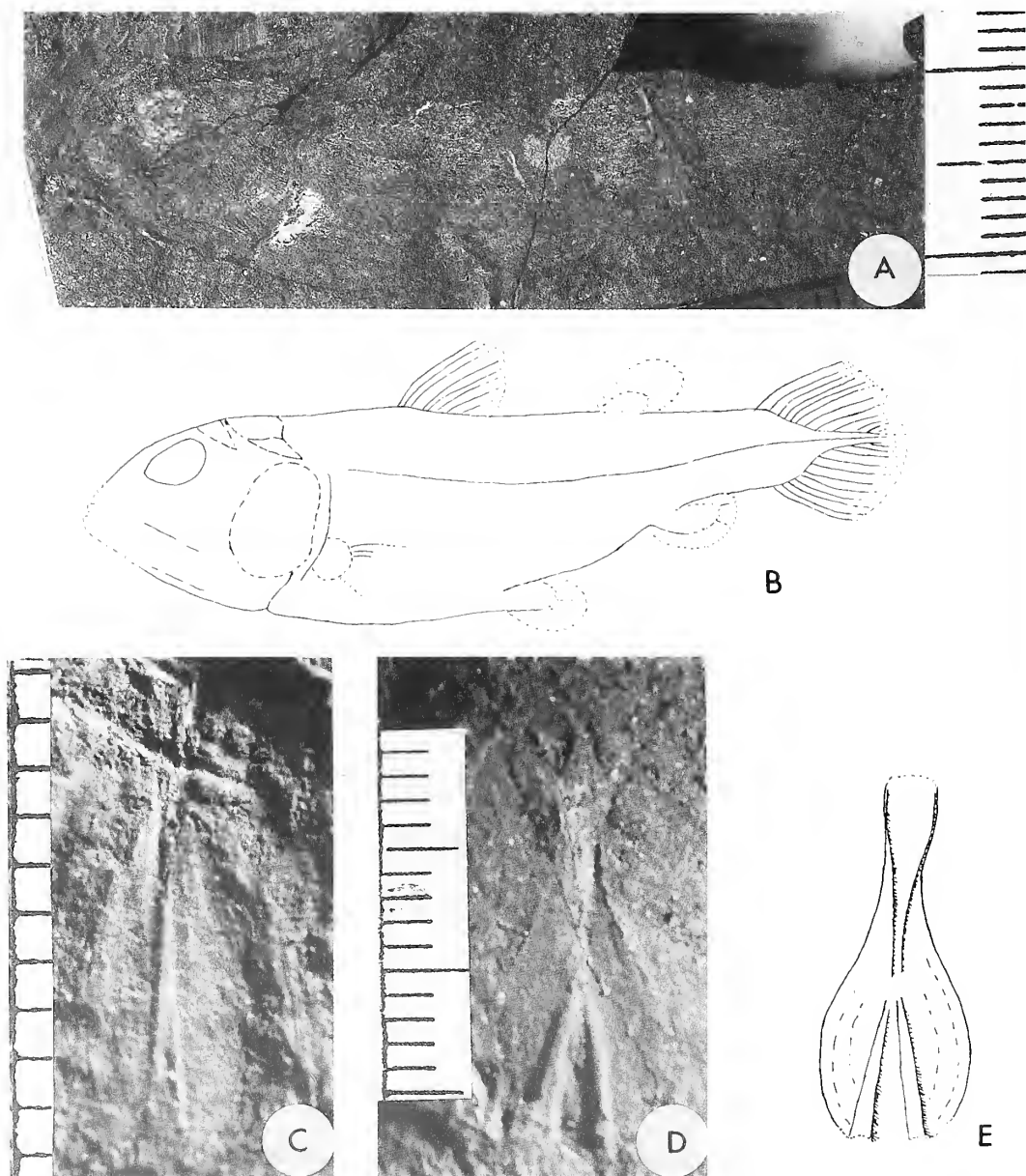


Fig. 59A-E: A. Whole bodied specimen of a juvenile coelocanth; B. Provisional interpretation of specimen in A (outline shortened and broadened through decay); C-D. Dorsal and ventral aspects of associated urohyal bones; E. Specimen in D.

third is an almost complete individual (Figs 57, 58A-C). This possibly represents the oldest known whole-bodied specimen of the group leading to holocephalomorphs (the paraselachomorphs) (pers. comm. J.A. Long, September 1994).

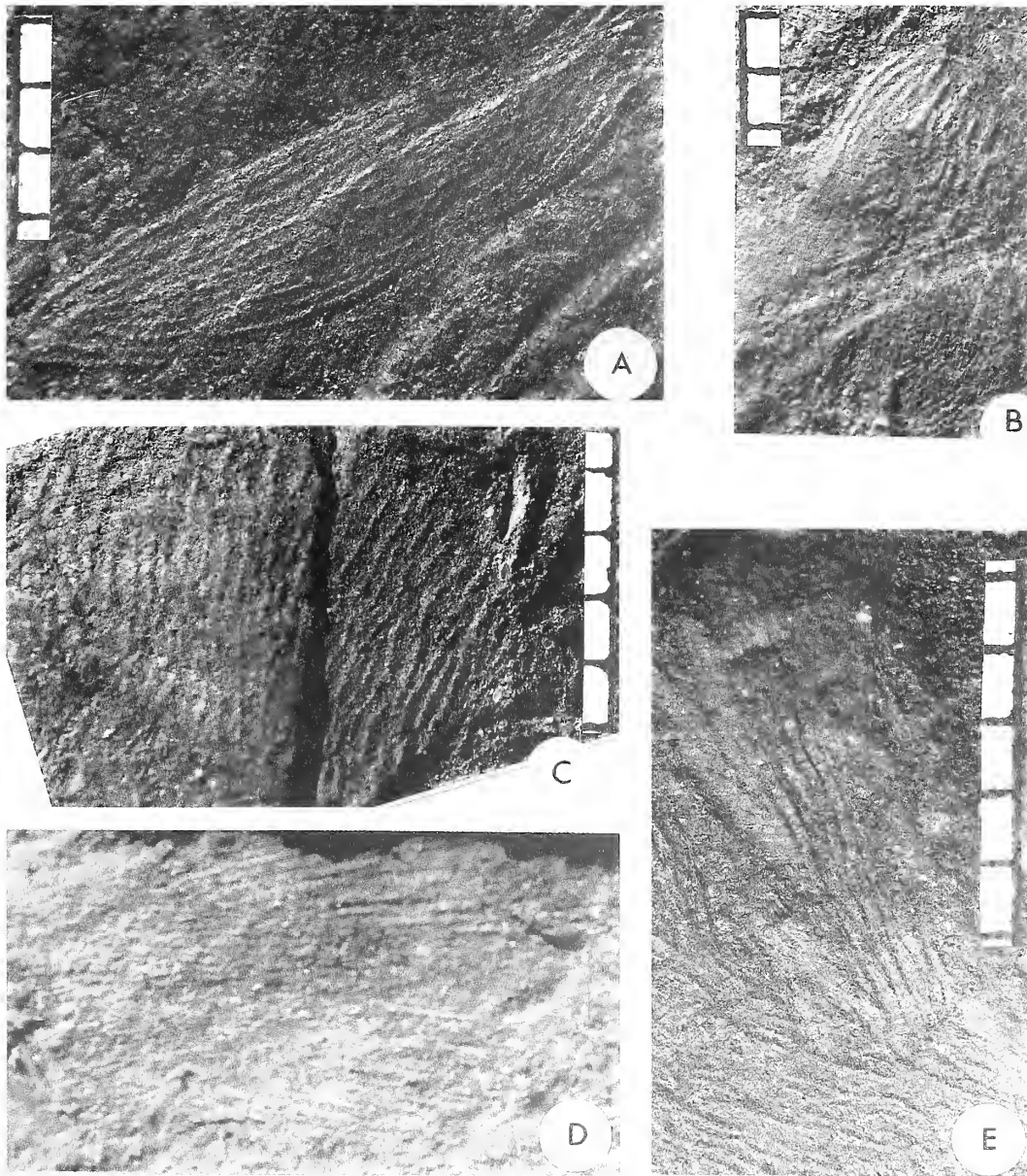


Fig. 60A-E. Juvenile coelocanth remains (scale in mm): A. Probable gular plate; B. Scale; C. Cheek plate; D. Detail of caudal fin of specimen in 59.A; E. First dorsal fin.

Crossopterygians (Figs 59-62, 63A-C)

The site has so far yielded the remains of about a dozen juvenile coelacanths (Figs 59, 60) (Anderson *et al.*, 1994). Most are complete although faintly preserved (Fig. 59A) but others are represented by disarticulated skull elements (Figs 59C-D, 60A, C). In addition, several isolated plates belonging to large individuals (pers. comm. J.A. Long, September 1994) have come to light (Fig. 62E-F).

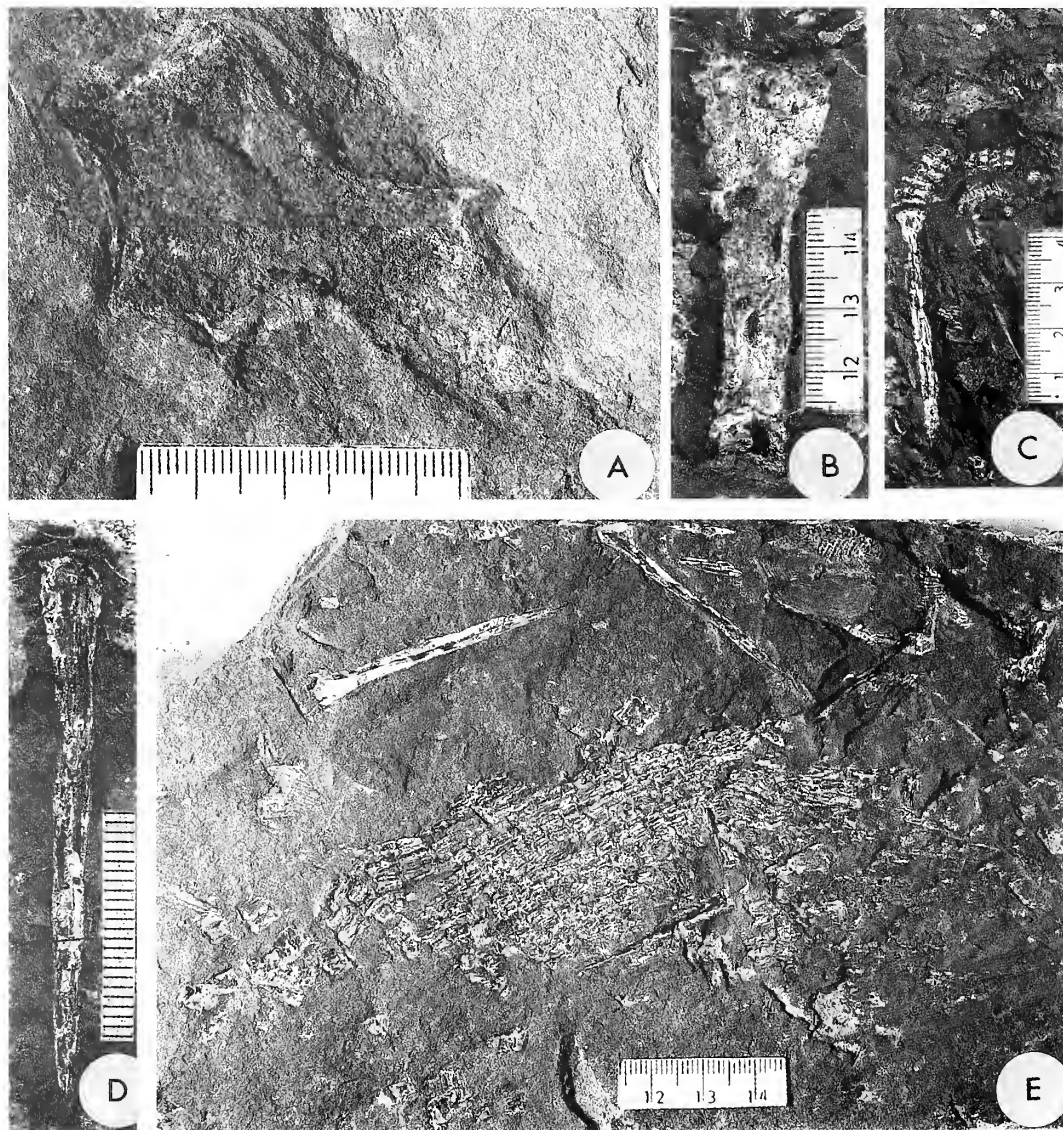


Fig. 61C-E. Rhipidistian fin remains: A. Ulnare; B. Fin basal; C-E. Supports (note body scale at top in E).

The highly disarticulated remains of a large osteolepiform rhipidistian, probably a eusthenopterid, have been recovered from a number of horizons. These include fin bones and rays (Fig. 61) and skull components (Fig. 62A-D); other isolated elements (Fig. 63A-C) may belong with this species.

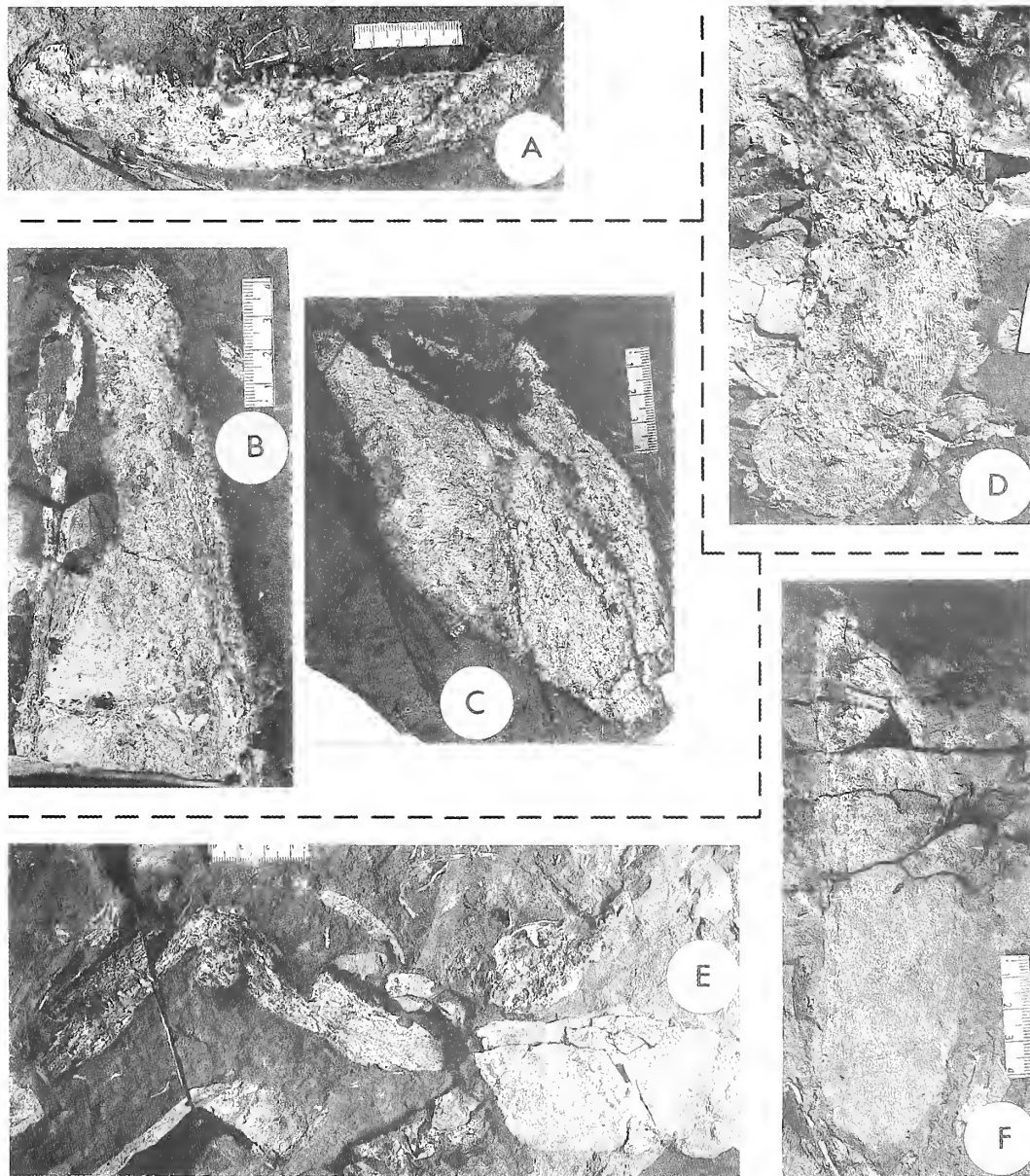


Fig. 62A-F: A. Rhipidistian lower jaw; B-C. Associated material; B. Crushed rhipidistian maxillary and possible palatoquadrate bones (anterior at top) (pers. comm. John Long); C. Rhipidistian ? cheek bone; D. Rhipidistian ? cleithrum part; E-F. Associated material of probable large coelocanth; E. Skull elements; F. ? Gular plate.

Dipnoans (Fig. 63D)

A single partial parasphenoid of a large lungfish is the sole representative of this group so far recovered from the site (Fig. 63D). It most closely resembles *Andreyevichthys* from Russia (Anderson *et al.*, 1994).

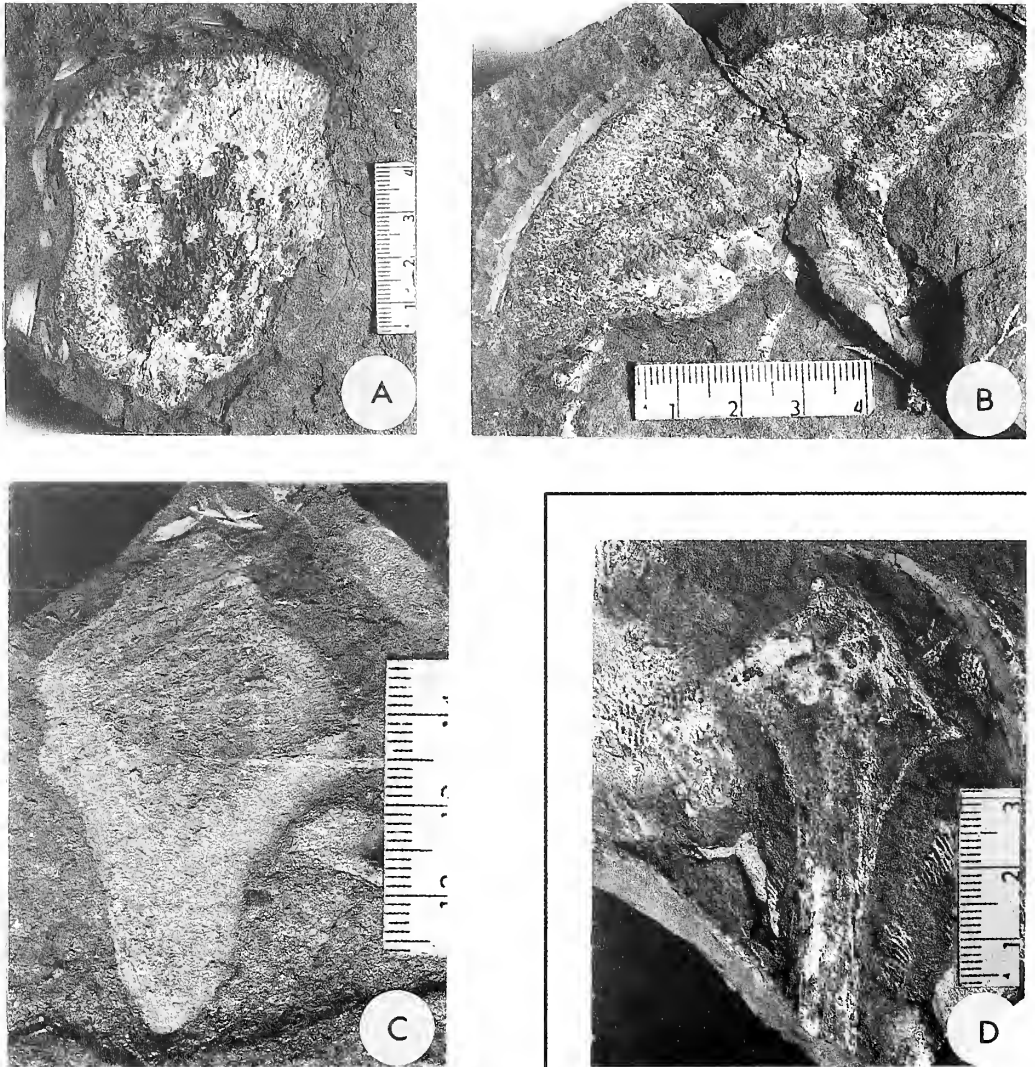


Fig. 63A-D: A. ?Rhipidistian operculum; B. ?Rhipidistian bone; C. ?Rhipidistian quadrato-jugal (pers. comm. John Long); D. Lungfish parasphenoid.

Incertae sedis (Fig. 64)

Among the other fish remains are elements that the authors cannot place within any of the above

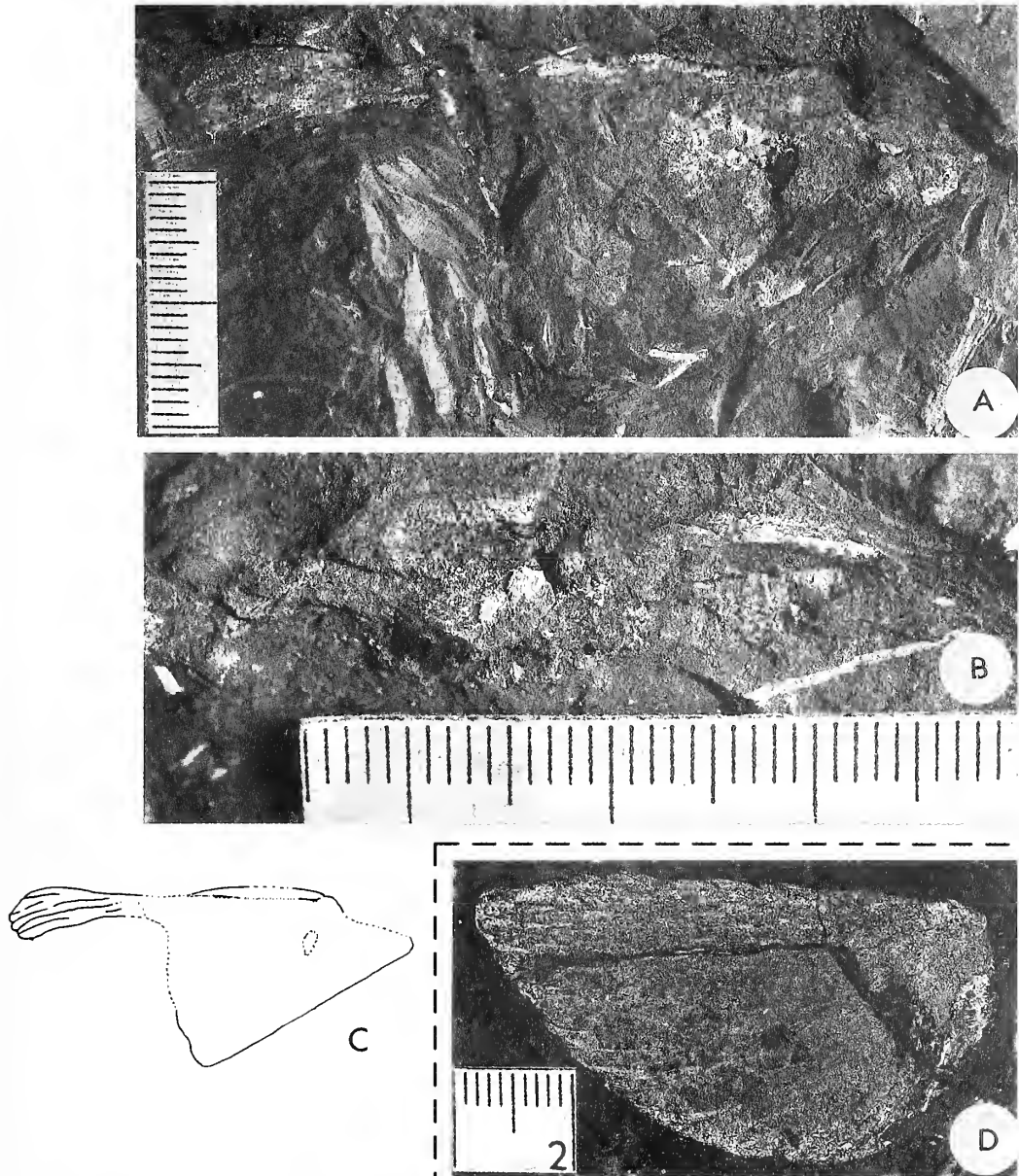


Fig. 64A-D. *Incertae sedis*: A. Poorly preserved specimen showing possible fin impression at left; B. Counter specimen of that in A showing possible dorsal spine; C. Outline of specimen in A; D. Isolated possible fin impression.

groups, including a poorly preserved specimen featuring a possible dorsal spine (Fig. 64A-C) and a possible isolated fin (Fig. 64D).

The presence of adult and juvenile fish material at the site suggests the possible use of the area

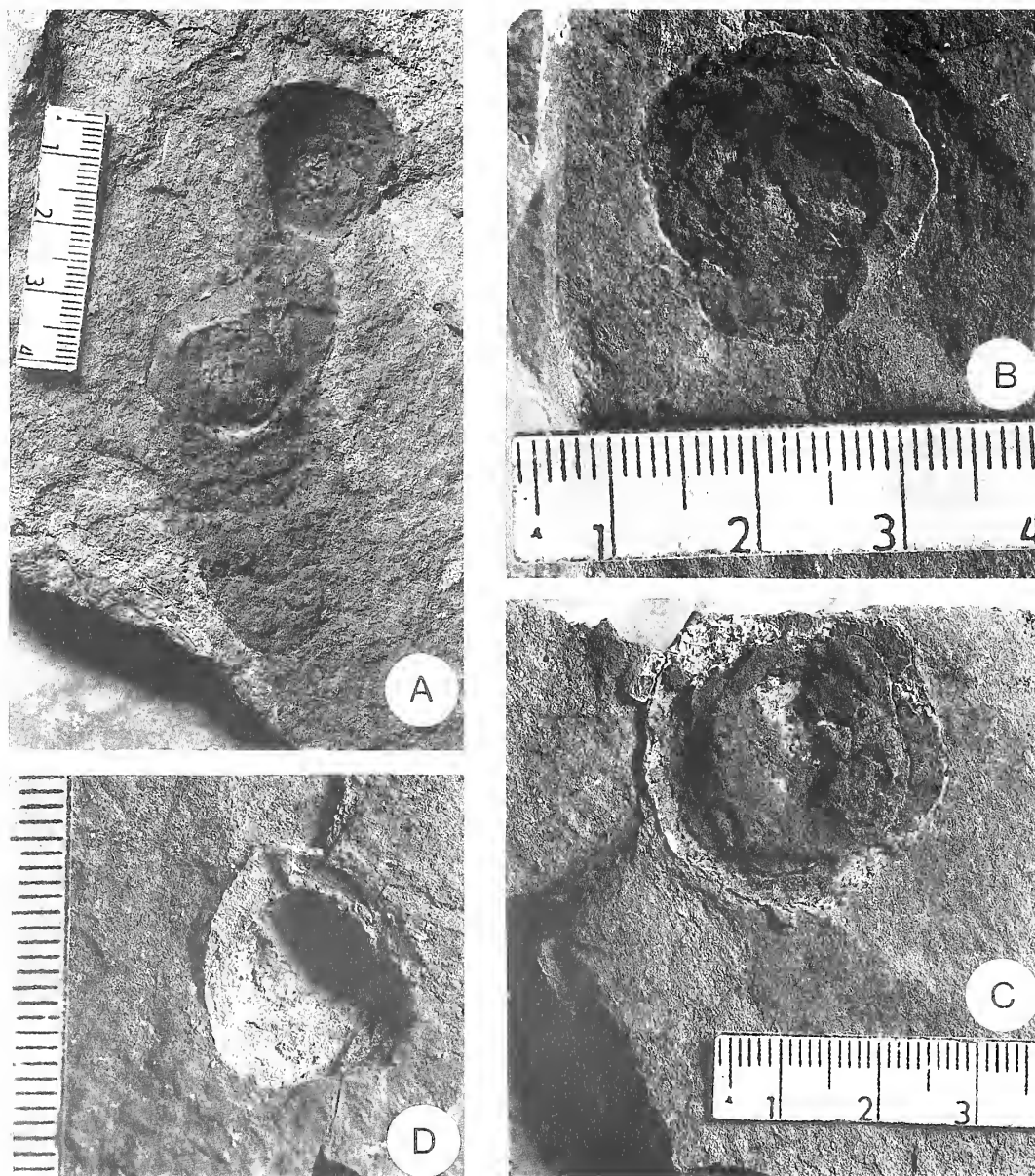


Fig. 65A-D. Possible priscean and/or eurypterid coprolites: A. Elongate specimen; B-C. Typical specimens; D. Specimen with carbonised material removed.

as a nursery by the fish in the manner of many extant fish species. Abundant carbonized helically spiral trace fossils (Fig. 65), some associated with fragmentary conchostracan and phaeophyte remains, are interpreted as the coprolites of fishes of a range of sizes. This would imply that at least some of the fish were living in the water column above the sediments and were not washed in after death from some other locality. Eurypterids are also known to have had spiral alimentary canals, and so it is possible that they may have been responsible for at least some of the apparent coprolites.

ACKNOWLEDGEMENTS

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Elsevier Press is thanked for permission to reproduce the photographs here presented as Fig. 4 A, B, C, D and E, Fig. 5 A-D, and Fig. 6 A and B appearing in Hiller and Gess (in press) and Fig. 1, Fig. 7 A-C and E, Fig. 8 A-E, Figs 9 and 10, Fig. 11 C and H, and Fig. 12 appearing in Gess and Hiller (in press).

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APPENDIX 1 - LIST OF FIGURED SPECIMENS

All material illustrated was collected from the site on the N2 bypass outside Grahamstown and is being deposited in the Albany Museum, Grahamstown. Most specimens are accompanied by counter specimens.

Fig. 3A-E: A. AM5264, R.W. Gess, 1993; B. AM5265, R.W. Gess, 1993; C. AM5266, R.W. Gess, 1993; D. AM5267, R.W. Gess, 1993; E. AM5292, R.W. Gess, 1994.

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- Fig. 4A-E:** **A.** AM5224, R.W. Gess, 1992; **B.** AM5225, R.W. Gess, 1993; **C.** AM5231, R.W. Gess, 1993; **D.** AM5229, R.W. Gess, 1993; **E.** AM5230, R.W. Gess, 1993.
- Fig. 5A-D:** **A.** AM5227, R.W. Gess, 1994; **B.** AM4843, F. Taylor, 1991; **C.** AM5226, R.W. Gess, 1994; **D.** AM5232, R.W. Gess, 1993.
- Fig. 6A-C:** **A.** AM5233, R.W. Gess, 1993; **B.** AM5223, R.W. Gess, 1993; **C.** AM5268, R.W. Gess, 1993.
- Fig. 7A-F:** **A.** AM5218, R.W. Gess, 1993; **B.** AM5219, R.W. Gess, 1994; **C.** AM5200, R.W. Gess, 1993; **D.** AM5201, R.W. Gess, 1993; **E.** AM5220, R.W. Gess, 1994; **F.** AM5269, R.W. Gess, 1993.
- Fig. 8A-E:** **A.** AM4849, R.W. Gess and F. Taylor, 1991; **B.** AM5206, R.W. Gess, 1993; **C.** AM5209, R.W. Gess, 1993; **D.** AM5207, R.W. Gess, 1993; **E.** AM5208, R.W. Gess, 1993.
- Fig. 11A-G:** **A-E,H.** AM5212, R.W. Gess, 1994; **F.** AM5214, R.W. Gess, 1993; **G.** AM5215, R.W. Gess, 1993.
- Fig. 12A-C:** **A.** AM5270, R.W. Gess, 1993; **B.** AM5271, R.W. Gess, 1993; **C.** AM5272, R.W. Gess, 1993.
- Fig. 13A-E:** **A.** AM5273, R.W. Gess, 1993; **B.** AM5274, R.W. Gess, 1993; **C.** AM5277, R.W. Gess, 1993; **D.** AM5276, R.W. Gess, 1993; **E.** AM5275, R.W. Gess, 1993.
- Fig. 14A-D:** **A-C.** AM5278, R.W. Gess, 1993; **D.** AM5279, R.W. Gess, 1993.
- Fig. 15A-D:** **A.** AM5280, R.W. Gess, 1993; **B.** AM5234, R.W. Gess, 1993; **C.** AM5254, R.W. Gess, 1993; **D.** AM5255, R.W. Gess, 1993.
- Fig. 16A-C:** **A.** AM5253, R.W. Gess, 1993; **B.** AM4854, F. Taylor, 1991; **C.** AM5281, R.W. Gess, 1994.
- Fig. 17A-F:** **A.** AM5282, R.W. Gess, 1993; **B.** AM5252, R.W. Gess, 1993; **C.** AM5251, R.W. Gess, 1993; **D.** AM5283, R.W. Gess, 1993; **E.** AM5284, R.W. Gess, 1993; **F.** AM5285, R.W. Gess, 1993.
- Fig. 18A-F:** **A.** AM5286, R.W. Gess, 1993; **B.** AM5287, R.W. Gess, 1993; **C.** AM5288, R.W. Gess, 1993; **D.** AM5289, R.W. Gess, 1994; **E.** AM5290, R.W. Gess, 1993; **F.** AM5291, R.W. Gess, 1993.
- Fig. 19A-I:** **A.** AM5260, R.W. Gess, 1993; **B.** AM5300, N. Hiller, 1992; **C.** AM5299, R.W. Gess, 1989; **D.** AM5297, R.W. Gess, 1994; **E.** AM5298, R.W. Gess, 1994; **F.** AM5301, R.W. Gess, 1993; **G.** AM5302, R.W. Gess, 1993; **H.** AM5303, R.W. Gess, 1993; **I.** AM5304, R.W. Gess, 1993.
- Fig. 20A-E:** **A-B.** AM5305, R.W. Gess, 1993; **C.** AM5306, R.W. Gess, 1993; **D.** AM5307, R.W. Gess, 1993; **E.** AM5308, R.W. Gess, 1993.
- Fig. 21A-D:** **A.** AM5257, R.W. Gess, 1993; **B.** AM4871, G. Englebrecht, 1992; **C.** AM5258, R.W. Gess, 1993; **D.** AM5259, R.W. Gess, 1993.
- Fig. 22A-E:** **A.** AM5310, R.W. Gess, 1994; **B.** AM5312, A. Absalon, 1992; **C.** AM4828, F. Taylor, 1991; **D.** AM5311, R.W. Gess, 1994; **E.** AM4832, R.W. Gess, 1988;
- Fig. 23A-H:** **A.** AM5314, R.W. Gess, 1994; **B.** AM5315, R.W. Gess, 1994; **C.** AM5316, R.W. Gess, 1994; **D.** AM4828, F. Taylor, 1991; **E.** AM5313, R.W. Gess, 1994; **F.** AM5317, N. Hiller, 1992; **G.** AM5318, R.W. Gess, 1993; **H.** AM4826, R.W. Gess, 1986.
- Fig. 24A-D:** AM5310, R.W. Gess, 1994.
- Fig. 25A-H:** **A.** AM4894(WM1029), R.W. Gess, 1993; **B.** AM5319, R.W. Gess, 1994; **C.** AM4825, R.W. Gess, 1991; **D-E.** AM5320, R.W. Gess, 1994; **F.** AM4894(WM1027), R.W. Gess, 1993; **G.** AM4894(WM1025), R.W. Gess, 1993; **H.** AM4894, R.W. Gess, 1993.
- Fig. 26A-D:** **A.** AM5321, R.W. Gess, 1993; **B.** AM5322, R.W. Gess, 1994; **C.** AM4833, F. Taylor, 1991; **D.** AM5323, R.W. Gess, 1993.
- Fig. 27A-E:** **A.** AM5324, R.W. Gess, 1993; **B.** AM5325, R.W. Gess, 1994; **C-D.** AM5326, R.W. Gess, 1994; **E.** AM5310, R.W. Gess, 1994.
- Fig. 28A-F:** **A.** AM5327, R.W. Gess, 1993; **B.** AM5328, R.W. Gess, 1994; **C.** AM5329, R.W. Gess, 1993; **D.** AM5330, R.W. Gess, 1993; **E.** AM5331, F. Taylor, 1991; **F.** AM5332, R.W. Gess, 1994.
- Fig. 29A-E:** **A.** AM5262, R.W. Gess, 1993; **B.** AM4834, F. Taylor, 1991; **C.** AM5334, R.W. Gess, 1993; **D.** AM5335, R.W. Gess, 1993; **E.** AM4837, R.W. Gess, 1991.
- Fig. 30A-H:** **A.** AM5263, R.W. Gess, 1993; **B.** AM5336, R.W. Gess, 1993; **C.** AM5337, R.W. Gess, 1993; **D.** AM5338, R.W.

- Gess, 1993; **E.** AM5339, R.W. Gess, 1993; **F.** AM5340, R.W. Gess, 1993; **G.** AM5341, R.W. Gess, 1993; **H.** AM5342, N. Hiller, 1992.
- Fig. 31:** AM4913, R.W. Gess, 1993.
- Fig. 32A-C:** **A.** AM4914-b, R.W. Gess, 1993; **B.** AM4916, R.W. Gess, 1993; **C.** AM4918, R.W. Gess, 1993.
- Fig. 33A-D:** **A.** AM4921-3a, R.W. Gess, 1993; **B.** AM4921-4a, R.W. Gess, 1993; **C.** AM4921-2, R.W. Gess, 1993; **D.** AM4923-1, R.W. Gess, 1993.
- Fig. 34A-E:** **A.** AM5294, R.W. Gess, 1993; **B.** AM5295, R.W. Gess, 1993; **C.** AM4842, F. Taylor, 1991; **D.** AM5296, R.W. Gess, 1993; **E.** AM5293, R.W. Gess, 1994.
- Fig. 35:** AM5343, R.W. Gess and N. Hiller, 1993.
- Fig. 36C-G:** AM5343, R.W. Gess and N. Hiller, 1993.
- Fig. 37A-D:** **A-C.** AM5343, R.W. Gess and N. Hiller, 1993; **D.** AM5344, R.W. Gess, 1993.
- Fig. 38A-D:** **A-B.** AM5345, R.W. Gess, 1994; **C.** AM5346, R.W. Gess, 1993; **D.** AM5347, R.W. Gess, 1993.
- Fig. 39A-F:** **A.** AM5348, R.W. Gess, 1993; **B.** AM5349, R.W. Gess, 1993; **C.** AM5350, R.W. Gess, 1993; **D.** AM5351, R.W. Gess, 1993; **E.** AM5352, R.W. Gess, 1993; **F.** AM5353, R.W. Gess, 1988.
- Fig. 40A-G:** **A.** AM5354, R.W. Gess, 1993; **B.** AM5355, R.W. Gess, 1993; **C.** AM5356, R.W. Gess, 1993; **D.** AM5358, R.W. Gess, 1993; **E.** AM5357, R.W. Gess, 1993; **F.** AM5359, R.W. Gess, 1993; **G.** AM5360, R.W. Gess, 1993.
- Fig. 41A-F:** **A.** AM5361, R.W. Gess, 1993; **B.** AM4857, F. Taylor, 1991; **C.** AM5363, R.W. Gess, 1993; **D.** AM5364, R.W. Gess, 1993; **E.** AM5365, R.W. Gess, 1993; **F.** AM5366, F. Taylor, 1991.
- Fig. 42A-F:** **A.** AM5367, R.W. Gess, 1993; **B.** AM5368, N. Hiller, 1992; **C.** AM5261, R.W. Gess, 1993; **D.** AM5369, R.W. Gess, 1993; **E.** AM5370, R.W. Gess, 1993; **F.** AM5371, R.W. Gess, 1993.
- Fig. 43A-G:** **A.** AM5373, R.W. Gess, 1993; **B.** AM5406, R.W. Gess, 1993; **C.** AM5374, R.W. Gess, 1993; **D.** AM5379, F. Taylor, 1991; **E.** AM5380, R.W. Gess, 1993; **F.** AM5381, R.W. Gess, 1993; **G.** AM5382, R.W. Gess, 1993.
- Fig. 44A-D:** **A.** AM5375, R.W. Gess, 1993; **B.** AM5376, R.W. Gess, 1993; **C.** AM5377, R.W. Gess, 1993; **D.** AM5378, R.W. Gess, 1993.
- Fig. 45A-C:** **A-B.** AM5383, R.W. Gess, 1993; **C.** AM4818, R.W. Gess, 1989.
- Fig. 46A-E:** AM4883, R.W. Gess, 1993.
- Fig. 47A-H:** AM4902, R.W. Gess, 1993.
- Fig. 48A-E:** **A-B.** AM4898, R.W. Gess, 1993; **C.** AM4893, R.W. Gess, 1993; **D.** AM4886, R.W. Gess, 1993; **E.** AM4895, R.W. Gess, 1993.
- Fig. 49A:** AM4875, R.W. Gess, 1993.
- Fig. 50A-J:** **A.** AM4819, R.W. Gess, 1991; **B.** AM4908, R.W. Gess, 1993; **C.** AM5387i, R.W. Gess, 1994; **D.** AM5388, R.W. Gess, 1994; **E.** AM5384, R.W. Gess, 1994; **F.** AM5385b, R.W. Gess, 1994; **G.** AM5385a, R.W. Gess, 1994; **H.** AM4238, R.W. Gess, 1994; **I.** AM4867, F. Taylor, R. Gess and M. Anderson, 1991; **J.** AM5386, R.W. Gess, 1994.
- Fig. 51B-D:** AM4907, R.W. Gess, 1993.
- Fig. 52A-F:** **A-B.** AM5247, R.W. Gess, 1993; **C-D.** AM5246, R.W. Gess, 1993; **E.** AM5242, R.W. Gess, 1993; **F.** AM5240, R.W. Gess, 1993.
- Fig. 53A-E:** **A.** AM4901, R.W. Gess, 1993; **B.** AM4885, R.W. Gess, 1993; **C.** AM4881, R.W. Gess, 1993; **D.** AM4897, R.W. Gess, 1993; **E.** AM4900, R.W. Gess, 1993.
- Fig. 54A-C:** AM4816, F. Taylor, M. Anderson and R. Gess, 1991.
- Fig. 55A-E:** **A,D.** AM4882, R.W. Gess, 1993; **B.** AM4888, R.W. Gess, 1993; **C.** AM4891, R.W. Gess, 1993; **E.** AM4889, R.W. Gess, 1993.
- Fig. 56A-E:** **A-D.** AM4892, R.W. Gess, 1993; **E.** AM4880, R.W. Gess, 1993.
- Fig. 57A-B:** AM4817, R. Gess and M. Stonestreet, 1990.
- Fig. 58A, C and D:** **A and C.** AM4817, R. Gess and M. Stonestreet, 1990; **D.** AM4866, R.W. Gess, 1988.
- Fig. 59A, C and D:** **A.** AM4912(BPCr1005a), R.W. Gess, 1993; **C.** AM4912(BPCr1001), R.W. Gess, 1993; **D.** AM4912(BPCr1045), R.W. Gess, 1993.
- Fig. 60A-E:** **A-C and E.** AM4912(BPCr1001), R.W. Gess, 1993; **D.** AM4912(BPCr1005a), R.W. Gess, 1993.

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- Fig. 61A-E:** **A.** AM4868, R.W. Gess, 1989; **B.** AM5389b, R.W. Gess, 1994; **C.** AM5390, R.W. Gess, 1994; **D.** AM5389d, R.W. Gess, 1994; **E.** AM5389ei, R.W. Gess, 1994.
- Fig. 62A-F:** **A.** AM5221, R.W. Gess, 1993; **B.** AM5391ai, R.W. Gess, 1993; **C.** AM5391bi, R.W. Gess, 1993; **D.** AM5389a, R.W. Gess, 1993; **E.** AM5392aii, R.W. Gess, 1993; **F.** AM5392b, R.W. Gess, 1993.
- Fig. 63A-D:** **A.** AM5393a, R.W. Gess, 1993; **B.** AM5249, R.W. Gess, 1993; **C.** AM5394a, R.W. Gess, 1993; **D.** AM4821, S. Coutouvides, 1989.
- Fig. 64A-D:** **A.** AM5395a, R.W. Gess, 1993; **B.** AM5395b, R.W. Gess, 1993; **D.** AM5396, R.W. Gess, 1987.
- Fig. 65A-D:** **A.** AM5397b, R.W. Gess, 1993; **B.** AM5398, R.W. Gess, 1993; **C.** AM5400, R.W. Gess, 1994; **D.** AM5399a, R.W. Gess, 1994.

APPENDIX 2 - LIST OF ADDITIONAL SPECIMENS

- Rusophycos* and *Cruziana*: AM5402A-Z, R.W. Gess, 1993; AM5403A-B, R.W. Gess, 1993.
- Spirophyton*-like traces: AM5404A-E, R.W. Gess, 1993-1994
- Hungerfordia* sp.: AM4844, F. Taylor, 1991; AM4846, F. Taylor, 1991; AM5228, R.W. Gess, 1993; AM5372AA-AZ, BA-BZ, CA-CU, R.W. Gess, 1985-1994; AM5405A-C, F. Taylor, 1991.
- cf. Yeaia* sp.: AM5268, R.W. Gess, 1993; AM5611-5612, R.W. Gess, 1993.
- Charophytes: new genus 1, new species 1:** AM5193-5199, R.W. Gess, 1993-1994; AM5205(1)-(10), R.W. Gess, 1993-1994; AM5346, R.W. Gess, 1994; AM5423, Hodgen Family, 1993; AM5424, R.W. Gess, 1993.
- Charophytes: new genus 1, new species 2 :** AM5202-5203, R.W. Gess, 1993; AM5204(1)-(4), R.W. Gess, 1993; AM5417-5418, R.W. Gess, 1994; *cf.* AM5407-5416, R.W. Gess, 1992-1994.
- Charophytes: new genus 2, new species 1:** AM5210, R.W. Gess, 1993; AM5211(1)-(20), R.W. Gess, 1992-1993; AM5419A-Z, R.W. Gess, 1992-1994; AM5420A-N, R.W. Gess, 1992-1994; AM5421A-D, F. Taylor, 1991; *cf.* AM5422A-L, R.W. Gess, 1992-1994
- Charophytes: new genus 2, new species 2:** AM5213, R.W. Gess, 1993; AM5216, R.W. Gess, 1993; AM5217(1)-(3), R.W. Gess, 1993.
- Waterweed: (cf. Fig. 12):** AM5425-5426, R.W. Gess, 1993-1994; AM5600, R.W. Gess, 1994.
- Dutoitia alfreda*: AM5427-5432, R.W. Gess, 1993-1994; AM5346, R.W. Gess, 1993.
- cf. Fig. 14:* AM5433-5437, R.W. Gess, 1993-1994; AM5438, F. Taylor, 1991; AM5613-5614, R.W. Gess, 1993.
- Zosterophyllopsida: with spheroids:** AM5439-5481, R.W. Gess, 1993-1994; AM5476, F. Taylor, 1991; AM5482-5483, F. Taylor, 1991; AM5501-5502, R.W. Gess, 1993.
- Zosterophyllopsida: cf. Fig. 18F:** AM5484-5486, R.W. Gess, 1993.
- ? Zosterophyllopsida: cf. rhizomes:** AM4831, F. Taylor, 1991; AM5488, F. Taylor, 1991; AM5489-5490, R.W. Gess, 1993; AM5491(*cf.* 5253), R.W. Gess, 1994; AM5492-5500, R.W. Gess, 1993-1994.
- Lycopsida: cf. Fig. 19:** AM5503-5504, R.W. Gess, 1994; AM5531-5532, R.W. Gess, 1994.
- Lycopsida: cf. Fig. 20:** AM5309, R.W. Gess, 1993; AM5505-5507, R.W. Gess, 1993-1994.
- Lycopsida: cf. Fig. 21:** AM4838, F. Taylor, 1991; AM5508-5516, R.W. Gess, 1993-1994; *cf.* AM5517, R.W. Gess, 1993.
- Leptophloeum australe: stems and bark:** AM5313, R.W. Gess, 1993; AM5518A-H, R.W. Gess, 1993; AM5519A-E, R.W. Gess, 1993; AM5520A-B, R.W. Gess, 1993; AM5524-5525, R.W. Gess, 1993; AM5526A-G, R.W. Gess, 1993-1994; AM5527-5529, R.W. Gess, 1993-1994.
- Leptophloeum australe: rooting base:** AM5521, R.W. Gess, 1993.
- Leptophloeum australe: ?rootlets:** AM5522A-D, R.W. Gess, 1993.
- ? Leptophloeum australe - decortication rhombs:** AM4894(BPWM1009, R.W. Gess, 1993; BP1013-BP1016, BP1026, BP1028, BP1030-1039), AM5530A-Q, R.W. Gess, 1994; AM5533, R.W. Gess, 1993; AM5615-5616, R.W. Gess, 1994.
- Longicatrix** sp.: AM5534, F. Taylor, 1991; AM5535, R.W. Gess, 1993.
- Haplostigma irregularis:** AM5523A-C, R.W. Gess, 1993.

- Axes with leaf/root bases:** AM5536, R.W. Gess, 1993; AM5537A-D, R.W. Gess, 1993; AM5538A-C, R.W. Gess, 1993; AM5539, H.M. Anderson, 1993; AM5617-5619, R.W. Gess, 1993-1994.
- Striated axes:** cf. Fig. 30H, 41F: AM4856, F. Taylor, 1991; AM5543, F. Taylor, 1991; AM5544-5546, R.W. Gess, 1993.
- Archaeopteris new species:** AM4921:1, 5-6, R.W. Gess, 1993; AM4923:2-3, R.W. Gess, 1993; AM4915, R.W. Gess, 1993; AM4917, R.W. Gess, 1993; AM4919-4922, R.W. Gess, 1993; AM5547A-E, R.W. Gess, 1993; AM5548A-H, R.W. Gess, 1993; AM5549A-M, R.W. Gess, 1993; AM5392, R.W. Gess, 1994; AM5620, R.W. Gess, 1993.
- ? Archaeopteris new species 2:** cf. Fig. 34: AM4841, F. Taylor, 1991; AM5550, R.W. Gess, 1993.
- Dutoitia maraisia:** AM4856, F. Taylor, 1991; AM4875, F. Taylor, 1991; AM5343B-C, F-K, M-Z, AA-AD, R.W. Gess and N. Hiller, 1993; AM5551-5556, R.W. Gess, 1993; AM5567, R.W. Gess, 1993.
- ? Progymnospermopsida:** cf. Fig. 38: AM4836, F. Taylor, 1991; AM5566, F. Taylor, 1991; AM5557-5565, R.W. Gess, 1993-1994; AM5568, R.W. Gess, 1993.
- Plant axis:** cf. Fig. 39C: AM5577, R.W. Gess, 1993.
- Plant axes:** cf. Fig. 39F: AM5569-5576, R.W. Gess, 1993.
- Plant axes:** cf. Fig. 40C: AM5582-5583, R.W. Gess, 1993; AM5584, F. Taylor, 1991.
- Plant axes:** cf. Fig. 40F: AM5594-5597, R.W. Gess, 1993-1994.
- Plant axes:** cf. Fig. 40G: AM5598, F. Taylor, 1991.
- Plant axes:** cf. Fig. 41E: AM5601-5610, R.W. Gess, 1993-1994.
- Plant axes with whorls:** cf. Fig. 40A-B: AM5578-5580, R.W. Gess, 1993-1994; AM5581, F. Taylor, 1991.
- Plant axis:** cf. Fig. 41A: AM5599, R.W. Gess, 1993.
- Trilete spores:** cf. Fig. 40D: AM4851, F. Taylor, 1991; AM4853, F. Taylor, 1991; AM5586A-Z, R.W. Gess, 1993-1994; AM5587A-I, R.W. Gess, 1993-1994.
- Fertile capsules:** cf. Fig. 40E: in whorls: AM5588-5589, R.W. Gess, 1993.
- Fertile capsules:** cf. Fig. 40E: AM5590-5593, R.W. Gess, 1993-1994.
- Eurypterid: limb fragments:** AM5621-5622, R.W. Gess, 1993-1994.
- Eurypterid fragments:** AM5623-5641, R.W. Gess, 1993-1994.
- Conchostracon:** AM5647A-Z, R.W. Gess, 1993-1994; AM5648A-Z, R.W. Gess, 1993-1994; AM5649A-Z, R.W. Gess, 1993-1994.
- Ostracod:** AM5642-AM5646, R.W. Gess, 1993-1994; AM5691, R.W. Gess, 1994.
- Arthrodire:** AM4879, R.W. Gess, 1993; AM4884, R.W. Gess, 1993; AM4886=4893, R.W. Gess, 1993; AM4890, R.W. Gess, 1993; AM4896, R.W. Gess, 1993; AM4899, R.W. Gess, 1993; AM4903-4906, R.W. Gess, 1993; AM5235=5237, R.W. Gess, 1993; AM5236, M. Stonestreet, 1993; AM5241=AM5248, R.W. Gess, 1993; AM5244, R.W. Gess, 1993; AM5650-5667, R.W. Gess, 1993-1994; AM5670, R.W. Gess, 1994; AM5686-5688, R.W. Gess, 1993-1994.
- Bothriolepis sp.:** AM4911, R.W. Gess, 1993; AM5239, N. Hiller, 1992; AM5668, R.W. Gess, 1994; AM5669, N. Hiller, 1992.
- Piscean spines:** AM5681-5683, R.W. Gess, 1993-1994.
- Chondrichthyes:** AM5243, R.W. Gess, 1993; AM5245, R.W. Gess, 1994.
- Actinistia: juveniles:** AM4912(BPCr1002-BPCr1004, BPCr1006, AMBPCr1010), R.W. Gess, 1993.
- Actinistia: adults:** AM4909i(scale), R.W. Gess, 1989; AM5675-5676, R.W. Gess, 1994; AM5697A-O(scales), R.W. Gess, 1993-1994.
- Rhipidistia:** AM4909a-h, k-l (scales), R.W. Gess, 1989; AM5389f-z, aa-ag, R.W. Gess, 1992-1994; AM5671, N. Hiller, 1992; AM5672-3, R.W. Gess, 1993; AM5674A-L(scales), R.W. Gess, 1985-1994.
- Pisces:** AM5677-5679, R.W. Gess, 1993; AM5680A-Q(scales), R.W. Gess, 1993-1994; AM5684-5685, R.W. Gess, 1994; AM5689, R.W. Gess, 1994.
- ?Piscean coprolites:** AM5401A-O, R.W. Gess, 1993-1994; AM5690, R.W. Gess, 1994.
- Other ?fecal material:** AM5642-5643, R.W. Gess, 1993; AM5691-5695, R.W. Gess, 1994.

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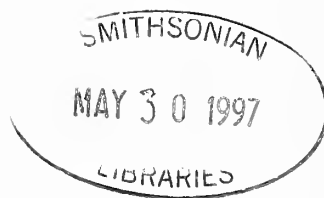
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Alien and translocated aquatic animals in southern Africa (excluding Zimbabwe and Mozambique) – revised checklist and analysis of distribution on a catchment basis

I.J. DE MOOR and M.N. BRUTON

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Alien and translocated aquatic animals in southern Africa (excluding Zimbabwe and Mozambique) - revised checklist and analysis of distribution on a catchment basis

by

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(J.L.B. Smith Institute of Ichthyology, Grahamstown, 6140 South Africa)

ABSTRACT

The distribution patterns of 44 alien and translocated freshwater aquatic animals in southern Africa (excluding Zimbabwe and Mozambique) are updated and re-assessed. A comparison with 1988 records indicates the presence of two alien species not previously recorded in natural waters. The distributions of five species, previously recorded in catchments outside their native ranges, have been extended into new catchments. The common carp *Cyprinus carpio* Linnaeus 1758 has invaded more catchments than any other species and its range has recently been extended into the Phongolo and upper Mkuze systems.

The composition of alien species in each major catchment and the catchments invaded by individual alien species are documented. Results indicate a positive correlation between the number of alien species and water availability in catchments. Regions with the highest number of alien species are associated with major urban centres. Records suggest that high numbers of alien species are found in regions with a low diversity of indigenous species, however, this trend could not be statistically validated. In eight out of 19 catchments/waterbodies investigated more than half of the fish species were aliens. In the Kei catchment 11 out of 13 fish species are aliens.

Certain waterbodies of high conservation status (Okavango, Lake Sibaya and the Mkuze Swamps) in sub-tropical regions are free of alien fish. Temperatures in these waterbodies are likely to be within the tolerance range of most tropical species associated with the aquarium trade. It is recommended that special measures be taken to prevent introductions of alien species into these systems. The presence of *Cyprinus carpio*, *Micropterus salmoides* (Lacepede 1802) and *Oreochromis mossambicus* (Peters 1852) in the Omatako drainage raises the possibility of the future introduction of these species into the Okavango system. Potential introductions through interbasin transfer schemes are also discussed.

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INTRODUCTION

Numerous ecological problems have resulted from the introduction of alien aquatic animals into inland waters in many parts of the world (Welcomme, 1988). These include the degradation of the environment due to habitat alteration, the disruption of the host community through competition with and predation on indigenous species, deterioration of fish stocks (through stunting of the introduced population), genetic contamination of the host community, and the introduction of parasites and diseases.

Serious economic and health problems have arisen as a result of some introductions. The recent introduction of the zebra mussel *Dreissena polymorpha* (Pallas 1771) into the Laurentian Great Lakes in North America has caused widespread economic damage as a result of its prolific growth in the water pipes of electricity-generation and water-treatment facilities (Griffith et al., 1991). The introduction of the malaria-vector mosquito *Anopheles gambiae* sensu lato Giles 1920 into South America resulted in a malaria epidemic causing the death of over 20 000 people (Soper and Wilson, 1943).

Bruton (1986) noted that the life-history style adopted by introduced species was an important factor in determining the success or failure of the introduction. Preliminary distribution records suggested that altricial fish (which produce small, incompletely developed young and are generalists capable of surviving in an unstable, uncrowded environment), such as rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) and the common carp *Cyprinus carpio*, had successfully invaded species-poor, abiotically harsh environments. Precocial species (which produce large, well-developed young and are specialists adapted to survive in a stable, crowded environment), such as the largemouth bass *Micropterus salmoides*, swordtail *Xiphophorus helleri* Heckel 1848, and the guppy *Poecilia reticulata* Peters 1859, tended to invade species-rich, biotically harsh environments. The present paper will attempt to evaluate some of these hypotheses.

De Moor and Bruton (1988) reviewed the problem in southern Africa and found that 58 alien species had naturalised breeding populations in the southern African region (excluding Zimbabwe and Mozambique). Of these, 33 were from other countries and 25 were transfers of species into new catchments within southern Africa. Of the 58 species which were frequently recorded in natural habitats, 37 were considered to be detrimental, three to be beneficial and 18 to be equivocal (i.e. beneficial in some respects and detrimental in others). Detrimental impacts included the alteration of the habitat, predation of and competition with indigenous species, the introduction of parasites, and the threat of genetic contamination (de Moor and Bruton, 1988). Although such impacts can be regarded as being significant in terms of environmental effects, alien aquatic animals in southern Africa have not yet caused any major medical or economic impacts on the scale of other well-known disasters mentioned above.

The aim of this paper is to provide an updated checklist of alien aquatic animals in southern Africa and to revise distribution records in terms of catchment distributions. This will enable conservation officials and other managers to rapidly assess the degree of invasion in each catchment

and to identify catchments which are susceptible to further invasions. Information from previous publications (Bruton, 1986; de Moor and Bruton, 1988) is also updated and re-assessed. It is hoped that the synthesis of distribution records presented in this paper will serve as a basis for further investigations into the biogeography and ecology of alien aquatic animals in southern Africa.

It should be noted that the invasion of freshwater ecosystems is an ongoing process and the present review represents a "snapshot" picture of known distribution records at present. There are notable gaps in distribution records, particularly with respect to fish parasites and certain popular angling species (such as *Cyprinus carpio*, *Micropterus salmoides*, and *Oreochromis mossambicus*) which have been illegally translocated into many catchments in southern Africa.

With the exception of the grass carp *Ctenopharyngodon idella* (Valenciennes 1844) (a long-lived species which does not breed in natural waters in southern Africa) only naturalised alien species are included in this review. The regions covered include South Africa, Lesotho, Swaziland, Namibia and Botswana. With the exception of the latter two countries, descriptions of major catchments (Fig. 1) follow the convention of the Department of Water Affairs (Anon, 1986). Appendix 1 describes the catchments and sub-catchments illustrated in Fig. 1, as well as the major rivers, impoundments and towns in each region.

Certain categories of species listed in de Moor and Bruton (1988) have been excluded from this review. These include: marine species; threatened species translocated to regions close to their native range; species translocated within the same major catchment; and biocontrol agents which have a beneficial impact on the environment.

A number of terms used in this publication are defined below.

The study area. This is indicated in Figure 1. The area includes all catchments south of the Limpopo and Cunene rivers as well as the Okavango region which forms part of the upper Zambezi catchment. For political reasons distribution records from Zimbabwe and Mozambique were not available during the time when work on this project was being carried out.

Natural and semi-natural habitats. For the purpose of this study this includes natural watercourses, large impoundments and small earthen impoundments either of which may overflow into natural waters during flood periods. Excluded from this definition are garden ponds, closed-system aquaculture installations and concrete farm reservoirs.

Alien species. A species which has been translocated, either intentionally or unintentionally, by man into catchments beyond its native range.

Translocated indigenous species. A species indigenous to the study area, which has been translocated by man into new catchments within the study area. Translocated species can be regarded as a special category of alien species.

Invasive species. An alien species which has spread unaided within freshwater ecosystems.

Naturalised species. An introduced species which has established self-sustaining populations in areas of natural or semi-natural vegetation or habitat.

Detrimental impact. The introduction has had a harmful impact on the environment.

Beneficial impact. The introduction has apparently had an advantageous impact on the environment. This term is confined to host-specific alien species introduced for the purpose of biocontrol, which successfully controlled the targeted host species.

Major catchments. Catchments categorised by the Department of Water Affairs (Anon, 1986) as major and here designated by letters of the alphabet (Fig. 1). In most instances these catchments are discrete and separated from other catchments by watershed boundaries. Exceptions are the Olifants and the Vaal (catchments B & C, Fig. 1) which represent major tributaries of the Limpopo and Orange



Fig. 1: The study area, indicating major catchments and sub-catchments (refer to Appendix 1 for information on major rivers, waterbodies and place names in each catchment).

ivers (catchments A & D, Fig. 1) respectively.

In some instances a number of small discrete coastal catchments (within major catchments G, K, M, P, R, T, U and W: Fig. 1) are categorised together as a "major catchment area".

Sub-catchments. Catchments of tributaries within major catchments, designated by numbers in Fig. 1.

Successful introduction. An introduction is described as successful where an alien species has established a naturalised population in natural or semi-natural waters.

Failed introduction. An introduction is regarded as unsuccessful or failed where an alien species has not succeeded in establishing a naturalised population, despite repeated introductions into natural waters.

METHODS

Distribution records were obtained from: the Albany Museum and the J.L.B. Smith Institute of

Ichthyology, Grahamstown (Appendices 2 and 3); literature records of species from accredited scientific journals and reports (Appendices 2, 3 and 4); and personal communications with nature conservation officials and other experts in the field (Appendices 2, 3 and 4).

Distribution records were categorised as follows.

S - Self-sustaining populations (=breeding populations).

P - Probable presence. Where no formal record has been received of the presence of a widespread species in a particular catchment sub-division but where such a species is widespread in an adjacent catchment it is considered that the presence of the species is "probable" in the catchment concerned.

R - Regularly stocked. Where the species is regularly stocked in a particular catchment but populations are probably not self-sustaining.

M - Possibly stocked. Where there are no definite records of stocking but it is suspected that the species may be stocked somewhere in the catchment. It is unlikely that self-sustaining populations occur in these catchments.

H - Historical. Where only isolated distribution records prior to 1985 exist so that it is not known whether self-sustaining populations are present.

B - Boundary. Where a self-sustaining population is found in a region close to the watershed boundary and consequently the catchment to which the locality belongs is uncertain.

* - New distribution record. Not recorded in de Moor and Bruton (1988).

Latitude/longitude co-ordinates were obtained from ordnance survey maps, the *Times World Atlas* or Skead (1973). The catchment associated with each record was then identified by reference to Fig. 1.

In the case of certain species it was possible to estimate abundance in selected catchments by reference to literature or through personal communication with researchers. If only one record exists of the species, then it was either classified as rare (if a recent record) or as an historical record. If museum records indicated that the species had been collected in a number of localities in at least three tributaries, or in more than four localities in the mainstream of rivers, then the species was classified as widespread within the catchment or sub-catchment.

Based on the above information, abundance was noted within certain sub-catchments and classified as follows (Tables 1 - 4).

1 - Very rare. Only a single record exists.

2 - Isolated populations in small restricted region/regions. These may, however, be thriving populations.

3 - Widespread. Found throughout the upper and lower catchment or sub-catchment.

3_u - Widespread in the upper catchment.

3_l - Widespread in the lower catchment.

It must be emphasised that records of abundance are incomplete, and have only been noted when the relevant information is available. This implies that the distribution of most alien species is greater than indicated by records summarised in Tables 1 - 4.

RESULTS

The checklists of alien and translocated indigenous species (Appendices 2 and 3 respectively) include brief notes on the native range, date of first introduction, impact, and abundance of each species, as well as code numbers indicating selected references (listed in Appendix 4). For further details see de Moor and Bruton (1988).

Table 1. Distribution records of alien aquatic animals present in catchments and sub-catchments A - G illustrated in Fig.1.

Species	Catchments																	
	A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3	D4	D5	D6	E	F	G
<i>Ichthyophthirius multifiliis</i>			S	S*	S													
<i>Bothriocephalus acheilognathi</i>					S			S										
<i>Trichodina acuta</i>	S		S		S			S	S									
<i>Craspedacusta sowerbyi</i>																		
<i>Argulus japonicus</i>	S							S	S									
<i>Cherax tenuimanus</i>																		
<i>Procambarus clarkii</i>																		
<i>Physa acuta</i>	S 3			S 3	S 3			S 3										S
<i>Helisoma duryi</i>																		H
<i>Lymnaea columella</i>	S 3		S 3	S 3	S 3	S		S 3	S			S				S		S 3
<i>Oncorhynchus mykiss</i>	R		M	S 2	R	S/R	S/R 2	M	M	S 3u	S 3u					S 2		S 2
<i>Salmo trutta</i>	M		M	S 2	M	S 2				S 2	R					S 2		S 2
<i>Carassius auratus</i>													S 1	S				S
<i>Ctenopharyngodon idellus</i>							M	R	M									
<i>Cyprinus carpio</i>	S 3	P	S 2	P	S 3	S	P	S 3	S 3		S	S	S	S	S	M		S 3
<i>Hypophthalmichthys molitrix</i> *					S*													
<i>Tinca tinca</i>																		S 1
<i>Gambusia affinis</i>	S*		H	S*				S										S*
<i>Poecilia reticulata</i>														S				
<i>Xiphophorus helleri</i>																		
<i>Lepomis macrochirus</i>			S		S		S	P	P		S	P				S 3		S 3
<i>Micropterus dolomieu</i>	S		S	S	P	S	P	S	P		P	P				S 3		S 3
<i>Micropterus punctulatus</i>											S* 1							H
<i>Micropterus salmoides</i>	S	P	S 2	S	S	S	S	S	S		S	S			S	S 3		S 3

Table 1. Continued.

Species	Catchments																	
	A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3	D4	D5	D6	E	F	G
<i>Perca fluviatilis</i>								S										S
<i>Oreochromis aureus</i>																		H
<i>Oreochromis niloticus</i>																		H
<i>Trachemys s. elegans</i>	S																	

Code for distribution

S - Self-sustaining populations

P - Self-sustaining populations probable, but no definite records

R - Regular stocking, probably not self-sustaining

M - Maybe stocked somewhere in catchment, self-sustaining populations unlikely

H - Historical. May or may not still be present

U - Uncertain historical translocation

* - New distribution record since de Moor & Bruton (1988)

Code for abundance

1 - Very rare. Probably a single record

2 - Isolated population in small restricted region/s

3 - Widespread

3_u - Widespread in upper catchment3_l - Widespread in lower catchment

B - Boundary: Close to watershed between two catchments, so exact catchment is uncertain

Tables 1 and 2 summarise the distribution of alien and translocated indigenous species (respectively) in catchments A-G. Tables 3 and 4 summarise the distributions of alien and translocated indigenous species (respectively) in catchments H-Z. The number of species in each sub-catchment and major catchment is also noted. Tables 3 and 4 also indicate the number of catchments (from A-Z) invaded by each species. It should be noted that in calculating these totals, only the "S" (species survives) and "R" (regularly stocked) categories of distribution records are considered. Historical records are noted separately.

DISCUSSION

Reclassification of distribution records

Species for which there were previously single distribution records (de Moor and Bruton, 1988) have now been classified as having "historical distributions" since no further reports have been received of their presence in natural waters (Tables 1 - 4). These species include two alien cichlids (*Oreochromis aureus* (Steindachner 1864) and *O. niloticus* (Linnaeus 1758)) previously recorded in Natal and the Western Cape, one alien crayfish (*Cherax tenuimanus* (Smith 1912)) previously recorded in the Buffalo River (Eastern Cape), and four translocated indigenous cichlids (*Oreochromis andersonii* (Castelnau 1861), *Sargochromis codringtoni* (Boulenger 1908), *Serranochromis thumbergi* (Castelnau 1861) and *S. augusticeps* (Boulenger 1907)) which were included in a group of species translocated into the Shashi impoundment from the Okavango region (Gilmore, 1978).

It should be noted that the term "historical" does not imply that the species has definitely disappeared from the region in question. In the context of this publication "historical" indicates that no further records have been received in the past 10 years, and it is possible that the species may still be present in the region.

Table 2. Distribution records of translocated indigenous aquatic animals present in catchments and sub-catchments A-G illustrated in Fig.1. Total numbers of alien species (including species listed in Table 1) in each catchment are also given.

Species	Catchments																	
	A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3	D4	D5	D6	E	F	G
<i>Barbus aeneus</i>																		
<i>Barbus auoplus</i>																		
<i>Labeo capensis</i>																		
<i>Labeo umbratus</i>				S														
<i>Clarias gariepinus</i>																		S
<i>Chetia flaviventris</i>						S*												
<i>Oreochromis andersouii</i>		H																
<i>Oreochromis macrochir</i>		S																
<i>Oreochromis mossambicus</i>	S														S ₃₁	S		S
<i>Sargochromis codringtoni</i>		H																
<i>Serranochromis thunbergi</i>		H																
<i>Serranochromis r. jallae</i>		H																H
<i>Serranochromis angusticeps</i>		H																
<i>Tilapia r. swierstrae</i>																		
<i>Tilapia sparrmanii</i>																S		S* ₃
<i>Saudelia capeusis</i>																S		
No. alien species in s-c	11	1 + 5H	7 + 1H	9	10	7	3	11	5	2	6	3	2	3	3	9	0	15 + 5H
No. alien species in m-c's	14			15			13			10						9	0	15

s-c = sub-catchment

m-c = major catchment

Code for distribution

S - Self-sustaining populations

P - Self-sustaining populations probable, but no definite records

R - Regular stocking, probably not self-sustaining

M - Maybe stocked somewhere in catchment, self-sustaining populations unlikely

H - Historical. May or may not still be present

U - Uncertain historical translocation

* - New distribution record since de Moor & Bruton (1988)

Code for abundance

1 - Very rare. Probably a single record

2 - Isolated population in small restricted region/s

3 - Widespread

3_u - Widespread in upper catchment

3_l - Widespread in lower catchment

B - Boundary: Close to watershed between two catchments, so exact catchment is uncertain

Table 3. Distribution records of alien aquatic animals present in catchments and sub-catchments H - Z illustrated in Fig.1. Total catchments (from A - Z) invaded by alien species is also given.

Species	Catchments																							Total No. Catch's In- vaded (A-Z)
	H	J	K	L	M	N	P	Q	R	S	T1	T2	T3	U	V	W1	W2	X1	X2	X3	Y1	Y2	Z	
<i>Ichthyophthirius multifiliis</i>									S	S									S					
<i>Bothriocephalus acheilognathi</i>														S*				S*		S				
<i>Trichodina acuta</i>									S															
<i>Craspedacusta sowerbyi</i>														S	2									
<i>Argulus japonicus</i>																			S					
<i>Cherax tenuimanus</i>									H	1														
<i>Procambarus clarkii</i>																			S*					
<i>Physa acuta</i>					S									S	3		S							
<i>Helisoma duryi</i>																								
<i>Lymnaea columella</i>	S		S		S	3		S	S		S		S	S	3	S	S	S	S	S	S			
<i>Oncorhynchus mykiss</i>	S	R	S	M			M	M	S	S	S	S	S	S	30	S	S	M	S	S	R			
<i>Salmo trutta</i>	S		S	2					S	S	M	M	M	S	2	S	M	M	M	S				
<i>Carassius auratus</i>	H				S		S*			S			S*	S*										
<i>Ctenopharyngodon idellus</i>											M	R*	R	R	R	M	R*							
<i>Cyprinus carpio</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	3	S	S	S	M	S	M	S	S	3
<i>Hypophthalmichthys molitrix</i> *																								
<i>Tinca tinca</i>	S							S																
<i>Gambusia affinis</i>			S	2																				

Table 3. Continued.

Species	Catchments																							Total No. Catch's In- volved (A-Z)
	H	J	K	L	M	N	P	Q	R	S	T1	T2	T3	U	V	W1	W2	X1	X2	X3	Y1	Y2	Z	
<i>Poecilia reticulata</i>													S*	S		S						S	S	Z
<i>Xiphophorus helleri</i>														S					S			S	B	5
<i>Lepomis macrochirus</i>	S		S	S*			S*	H	S	S		S*	S	S	S	H		S*	S	S				19 16
<i>Micropterus dolomieu</i>	S	S*	S	S	S				S	S	S			S	S									17 15
<i>Micropterus punctulatus</i>							S	S*	S*	S		S*		S	S									8 8
<i>Micropterus salmoides</i>	S	S	S	S	S	H	S	H	S	S	P	S	S	S	S	S	S*	S*	S	S	S	S	S	32 21
<i>Perca fluviatilis</i>									S			S*												4 4
<i>Oreochromis aureus</i>													H											2H
<i>Oreochromis niloticus</i>													H											2H
<i>Trachemys s. elegans</i>														S										2 2

s-c = sub-catchment

m-c = major catchment

Code for distribution

S - Self-sustaining populations

P - Self-sustaining populations probable,

but no definite records

R - Regular stocking, probably not self-sustaining

M - Maybe stocked somewhere in catchment,

self-sustaining populations unlikely

H - Historical. May or may not still be present

U - Uncertain historical translocation

* - New distribution record since de Moor & Bruton (1988)

Code for abundance

1 - Very rare. Probably a single record

2 - Isolated population in small restricted region/s

3 - Widespread

3₀ - Widespread in upper catchment3₁ - Widespread in lower catchmentB - Boundary: Close to watershed between two catchments,
so exact catchment is uncertain

Table 4. Distribution records of translocated indigenous aquatic animals present in catchments and sub-catchments H-Z illustrated in Fig.1. Total numbers of alien species (including species listed in Table 3) and total numbers of catchments (from A-Z) invaded by alien species are also given.

Species	Catchments																							Total No. Catch. s In- vaded (A-Z)	
	H	J	K	L	M	N	P	Q	R	S	T1	T2	T3	U	V	W1	W2	X1	X2	X3	Y1	Y2	Z		
	S						S	S	S	S					S*										
<i>Barbus aeneus</i>		S					S	S		S															
<i>Barbus anoplus</i>													S*	H	H							S			
<i>Labeo capensis</i>								S							S*										
<i>Labeo umbratus</i>									S						H*	1									
<i>Clarias gariepinus</i>						S		S	S	S															
<i>Chetia flaviventris</i>																						1	1		
<i>Oreochromis andersonii</i>																							1H		
<i>Oreochromis macrochir</i>																							1	1	
<i>Oreochromis mossambicus</i>	S			S	S	3																S	S	9	
<i>Sargochromis codringtoni</i>																							3	3	
<i>Serranochromis thunbergi</i>																								1H	
<i>Serranochromis r. jallae</i>														S		H	S							2	2
<i>Serranochromis angusticeps</i>														1			1								1H
<i>Tilapia r. swierstrae</i>																								2	2
<i>Tilapia sparrmanii</i>	S	S	S*	S	S	S	S	S	S	S*	S*	P	P	S								S		15	15
<i>Sandelia capensis</i>							S							S*	S*									2	2
Total No. alien species in s-c	10	6	9	5	8	5	9	7	14	12	5	7	11	18	10	4	7	5	10	5	0	3	5		
Total No. in m-c's	10	6	9	5	8	5	9	7	14	12	14	14	14	18	10	8	11								

Legend. As for Table 1.

Table 5. Updated distribution records (compared to de Moor and Bruton, 1988).

Species	Range extensions (catchments) (Fig. 1)	No. catchments where new distributions recorded		Distribution code
		s-c	m-c	
<u>Species not previously recorded in study area</u>				
<i>Chetia flaviventris</i>	B3	1	1	NR
<i>Hypophthalmichthys molitrix</i>	B2	1	1	NR
<i>Procambarus clarkii</i>	X2	1	1	NR
<u>New distributions of species previously recorded in study area</u>				
<i>Bothriocephalus acheilognathi</i>	U,X1	2	2	RE
<i>Carassius auratus</i>	P,T3,U	3	3	CE
<i>Ctenopharyngodon idellus</i>	T2,W2	2	2	CE
<i>Cyprinus carpio</i>	W2	1	1	RE
<i>Poecilia reticulata</i>	T3	1	1	CE
<i>Lepomis macrochirus</i>	L,P,T2,	4	4	CE
<i>Micropterus punctulatus</i>	D2,Q,R,T2,	4	4	CE
<i>Micropterus salmoides</i>	W2,X1	2	2	CE
<i>Perca fluviatilis</i>	T2	1	1	CE
<i>Barbus aeneus</i>	V	1	1	RE
<i>Barbus anoplos</i>	T3	1	1	CE
<i>Labeo capensis</i>	V	1	1	RE
<i>Labeo umbratus</i>	V*	1	1	RE
<i>Tilapia r. swierstrae</i>	T3, U	1	1	CE
<i>Tilapia sparrmanii</i>	G,K,S,T1	4	4	CE

s-c - sub-catchments

m-c - major catchments

NR - New records: alien species not previously recorded in natural waters in the study area.

CE - Records which are probably the result of greater collection effort. Unlikely to represent a range extension of the species.

RE - New distribution records which represent probable range extensions of existing alien species.

* - Only a single specimen was collected: may not have established a population, so record is classified as historical (H) (Table 2)

New species and range extensions of naturalised species.

Table 5 summarises new records (NR) of three species (two alien and one translocated indigenous species) not previously recorded, as well as apparent range extensions (into new catchments or sub-catchments) of 15 alien species which were listed in de Moor and Bruton (1988). The latter records are classified as either new records as a result of greater collection effort (CE) or as probable range extensions (RE).

The two recently-recorded alien species (*Procambarus clarkii* (Girard 1852) and *Hypophthalmichthys molitrix* (Valenciennes 1844)) were previously present in southern Africa but kept in captivity. *Procambarus clarkii* was illegally imported through the aquarium trade, reports having been received of its presence in various retail outlets (Anon, 1987). It was first recorded from the Crocodile River (Nkomati system) in 1993 (Schoonbee, 1993). *Hypophthalmichthys molitrix* was widely distributed in aquaculture ponds but has not been previously recorded from natural waters.

The new record of a translocated indigenous species, *Chetia flaviventris* Trewavas 1961 (the canary kurper) (Table 5), is probably the result of an unrecorded translocation. Its presence has recently been noted in the B3 catchment (Fig. 1) (Hoffman, pers. comm.).

Of the new distribution records of previously-recorded alien species (Table 5), the apparent range extensions of ten species are probably the result of greater collection effort. In the case of five species (*Bothriocephalus acheilognathi* Yamaguthi 1934, *Barbus aeneus* (Burchell 1822), *Cyprinus carpio*, *Labeo capensis* (Smith 1841) and *L. umbratus* (Smith 1841)) the records probably represent true range extensions (Table 5). *Cyprinus carpio* has recently been recorded for the first time in the Mkuze system (Albany Museum records) in the W2 catchment. Its range within the W1 catchment has also been extended. Previously there was a single record of this species in the Phongolo floodplain at Tete Pan (de Moor and Bruton, 1988). It has now been recorded at numerous localities in this region (Merron, pers. comm.). Three other species (*B. aeneus*, *L. capensis* and *L. umbratus*) were recently recorded in the Kilburn Dam (Tugela system), the outlet of the Vaal-Tugela Interbasin transfer (IBT) scheme (Coke, pers. comm.).

The new distribution records of *B. acheilognathi* and *C. carpio* are cause for concern. The spread of the former species, a fish parasite, is highly undesirable and its extension into four major catchments less than 20 years after its initial introduction into southern Africa (Brandt et al., 1981) indicates that it is highly invasive. *Cyprinus carpio* has been in southern Africa for over 200 years (Bruton and van As, 1986) and has invaded most major catchments. The lowland region of northern Zululand (W1 and W2 catchments) was one of the few areas not yet invaded by this species. Carp has now extended its range into both of these catchments. Its presence in the upper Mkuze system (W2) is of particular concern, since it raises the possibility that this species may invade the Mkuze Swamps region which is a relatively pristine area (river conservation map associated with O'Keeffe, 1986).

Degree of invasion of catchments

The population size of alien species in comparison with that of indigenous species is probably the best estimate of the degree of invasion. The presence or absence of the alien species does not give a true reflection of the degree of invasion, since a small isolated population in a single locality would carry the same weighting as a species with a high population density throughout the catchment. Since information on population densities of alien species is not readily available for all catchments in the study area, discussion will be confined to certain trends.

The total number of alien species in sub-catchments and small major catchments (in sequence from the highest to the lowest number) and the areas of the catchments are listed in Table 6. Based on these figures, catchments were categorised into four classes according to the number of alien species present (Fig. 2). Although Table 6 indicates that certain regions, such as the Okavango, are free of alien aquatic animals, this must be seen in the context of this study (which excludes successful biocontrol agents and threatened species translocated to sub-catchments close to their native range). Certain biocontrol agents (i.e. two species of aquatic weevils, *Cyrtobagous salviniae* Calder & Sands 1985 and *C. singularis* (Hustache 1929)) have established populations in the Okavango (Schlettwein,

Table 6. Total number of alien species present in smaller catchments and in all sub-catchments (listed in sequence from the highest to the lowest number). Where figures are available*, the mean annual runoff (MAR), area of catchment, and MAR/unit area are also listed.

Catchment	MAR p.a. (10 ⁶ x m ³)	Area (km ²)	MAR/ unit area (10 ⁶ x m ³ /100km ²)	Total no. alien species
U - Mgeni	3174	18 267	17.38	18
G - Berg - W. Cape	2158	25 415	8.49	15
R - Buffalo	601	7 984	7.53	14
S - Kei	1064	20 535	5.18	12
T3 - Natal S. coast	1932	8 876	21.77	11
A1 - Upper Limpopo	916	43 244	2.12	11
C2 - Vaal - middle	1494	69 504	2.15	11
V - Tugela	4589	28 966	15.84	10
B2 - Olifants (Limpopo) - Elands	409	20 939	1.95	10
H - Bree	1954	15 658	12.48	10
X2 - Nkomati - Crocodile	1238	10 455	11.84	10
B1 - Olifants (Limpopo)- upper	1438	21 354	6.73	9
E - Olifants (W. Cape)	1015	48 880	2.08	9
K - S. Coastal	1372	7 227	18.98	9
P - Bushmans/Kariega	102	5 569	1.83	9
M - Swartkops	129	2 536	5.09	8
A3 - Limpopo (Levuvhu)	1374	66 360	2.07	7
B3 - Olifants (Limpopo) - Letaba	1344	31 241	4.30	7
Q - Fish	529	30 245	1.75	7
T2 - Transkei	4008	23 522	17.04	7
W2 - Zululand	2349	27 912	8.42	7
D2 - Orange - Caledon & NE Cape	6465	64 931	9.96	6
J - Gouritz	539	45 028	1.20	6
C3 - Vaal - lower	705	88 234	0.80	5
L - Gamtoos	504	34 790	1.45	5
N - Sundays	200	21 056	0.95	5
T1 - Transkei - southern	2018	11 497	17.52	5
X1 - Nkomati - Sabie	883	9 423	9.37	5
Z - Namibia - Swakop/Kuiseb	--	--	--	5
W1 - Swaziland - Usuthu, Phongolo	3545	32 360	10.95	4
X3 - Nkomati - Komati	1443	11 279	12.79	5
C1 - Vaal - upper	2288	38 609	5.93	3
D3 - Orange - middle	585	107 393	0.54	3
D5 - Orange - N. arid tributaries	202	111 111	0.18	3
D6 - Orange - lower	--	--	--	3
Y2 - Namibia - Omatako	--	--	--	3
D1 - Orange - upper	--	--	--	2
D4 - Orange - s. tributaries	268	93 690	0.29	2
A2 - Limpopo - Botswana tributaries	--	--	--	1
F - West coast (W. Cape)	110	28 629	0.38	0
Y1 - Okavango	--	--	--	0

* Department of Water Affairs statistics (Anon, 1986)

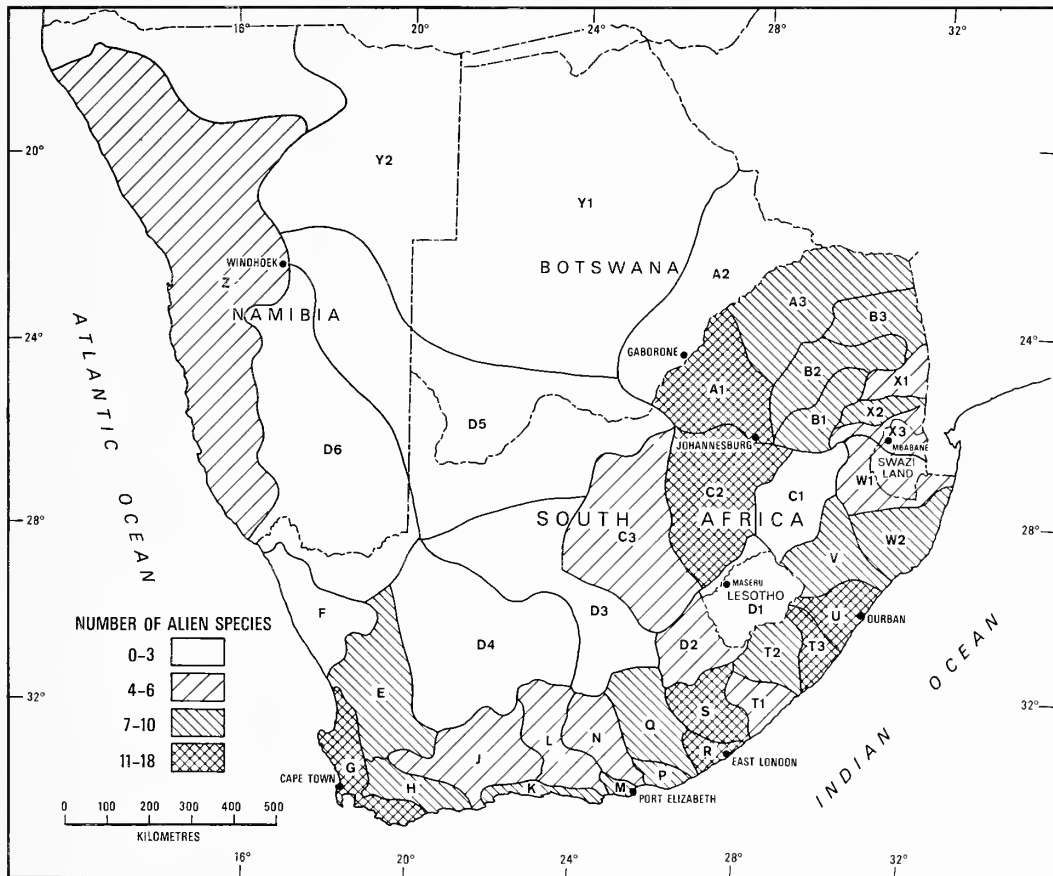


Fig. 2: Map of catchments in the study area illustrating the total numbers of alien species in each catchment or sub-catchment.

1985; de Moor and Bruton, 1988).

Regions with the highest number of alien species are associated with the major urban centres of the Pretoria-Witwatersrand region (catchments A1, C2), Cape Town (catchment G), Durban (catchment U) and East London (R) (Fig. 2). Low numbers of alien species are associated with sparsely populated regions in the high-altitude upper catchments of the Vaal and Orange (C1 and D1) or with the sparsely populated, arid regions (middle and lower Orange, West Cape coast, Botswana and Namibia). There are two noticeable exceptions to this trend. The Kei catchment (S) and the Natal south coast catchment (T3) have high numbers of alien species present (12 and 11 respectively) and neither is associated with major urban centres. It could also be expected that the Port Elizabeth region (catchment M) would have a higher number of alien species. The number of alien species in the catchment (8) is, however, high in relation to the size of the catchment (Table 6).

To test the relationship between the number of alien species present and water availability, a scattergram (based on data from Table 6) of the number of species present vs. mean annual runoff/unit area in 35 sub-catchments was constructed (Fig. 3). Correlation analysis (using Spearman's Rank

correlation test) indicates a positive relationship ($r = 0.45$) which is significant at the 0.01 level ($P = 0.009$; $n = 35$).

A number of experts in the field of invasive ecology (Elton, 1958; Fox and Fox, 1986) have noted a general tendency for relatively pristine ecosystems with a high diversity of species to have a greater resistance to invasion than is the case for less diverse or disturbed ecosystems. Since information on

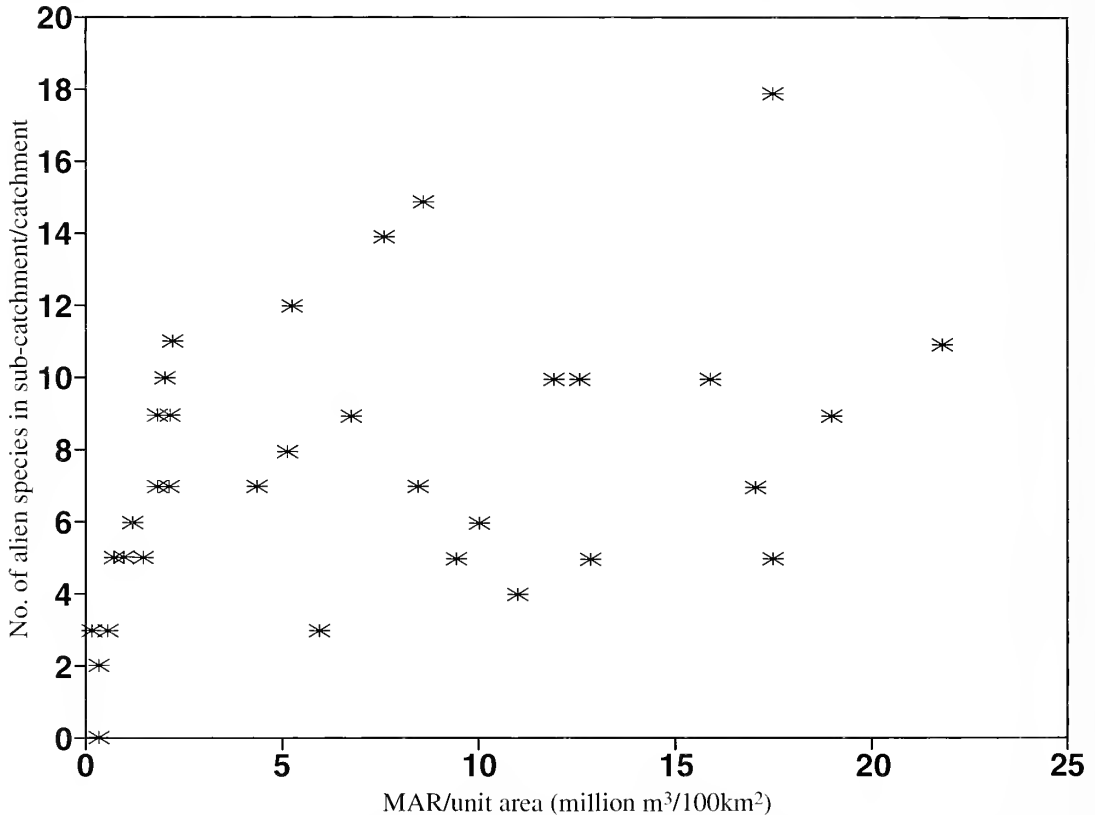


Fig. 3: Scattergram analysis of the total number of alien aquatic animal species present in individual catchments and sub-catchments vs. mean annual runoff (MAR) per unit area (million m³/100km²) in 35 catchments in southern Africa.

the number of indigenous aquatic invertebrates is not readily available, analysis was confined to a comparison of fish species present in the study area. Information on the species composition of indigenous fish (excluding diadromous species) in 19 selected waterbodies and catchments was obtained from a number of sources (Crass, 1966; Scott and Hamman, 1984; Skelton et al., 1985; Skelton, 1988, 1993; Bruton, 1993; Skelton, pers. comm.) and compared to the number of alien fish species present in the catchments concerned (Table 7). Results indicate that in eight of these catchments/waterbodies alien species represented over 50% of the total number of fish species present (Table 7). The Kei catchment, in which only two indigenous non-diadromous fish species have been found (Skelton, pers. comm.), had the greatest proportion of alien fish (84.6% of the total number of species) (Table 7).

Examination of Table 7 suggests a trend in which catchments or waterbodies with a high diversity of indigenous species (e.g. the Okavango region, the Phongolo system, Mkuze and Lake Sibaya) have fewer alien species than those with a low diversity of indigenous species (e.g. Kei, Great Fish, Sundays and Berg). In this context it should be noted that the two alien species recorded in the Phongolo system (*Oncorhynchus mykiss* and *Cyprinus carpio*) are relatively rare in the system. The former species is only found in a few small tributaries in the upper catchment and *C. carpio* has only been recorded in some isolated localities (Pongolapoort impoundment and in some regions of the Phongolo floodplain) where the population size is reported to be low (de Moor and Bruton, 1988; Merron, pers. comm.). Carp has, however, recently increased its range in this region (Merron, pers. comm.).

Correlation analysis of the number of alien fish species vs. number of indigenous fish species within catchments indicates no significant relationship between these two variables ($r_s = 0.28$; $P = 0.23$; $n = 19$). These results are based on total numbers of species within major catchments, since data on species diversity of sub-catchments were not available. Should this information become

Table 7. Comparison of the number of indigenous and alien fish species in selected catchments and waterbodies.

River system	No. alien fish species	No. indigenous fish species*	Alien fish species as % of total fish fauna
A. & B. Limpopo (incl. Olifants)	12	48	20.0%
C/D. Orange/Vaal	13	15	46.4%
X. Incomati	6	49	10.9%
Phongolo	2	43	4.4%
Mkuze system	2	25	7.4%
Lake Sibaya	0	19	0.0%
U. Umgeni	13	8	61.9%
V. Tugela	10	14	41.7%
R. Buffalo/Keiskamma	11	5	68.8%
S. Kei	11	2	84.6%
Q. Great Fish	6	4	60.0%
N. Sundays	3	4	42.9%
L. Gamtoos	5	6	45.5%
J. Gouritz	6	6	50.0%
H. Bree	9	4	69.2%
Berg	9	4	69.2%
E. Olifants	8	10	44.4%
P. Bushmans/Kariega/Kowie	9	6	60.0%
Okavango Delta	0	80	0.0%

* This figure excludes diadromous species

available, it would be possible to refine the resolution of the analysis. An increase in the number of samples would also improve the statistical validity of the correlation test and might produce a more significant result.

Many factors influence the degree of invasion of catchments, such as the opportunity of species to invade, niche space and habitat availability in the target environment (Stauffer, 1984). The question of susceptibility of catchments to invasion is therefore extremely complex. Further analysis of this topic would require a multivariate analysis of the factors which influence the success or failure of invasions. This is beyond the scope of the present study.

Invasive species

The number of major catchments invaded by alien and translocated indigenous species is summarised in Tables 8 and 9 respectively. The number of sub-catchments where certain species are reported to have a widespread distribution (Tables 8 and 9) as well as the number of catchments within the study area which are beyond the native range of translocated indigenous species (Table 9) have also been noted. The latter was calculated by subtracting the number of catchments in the native range (after Skelton, 1993) from the total number of catchments in the study area.

The species listed as widespread in certain catchments (*C. carpio*, *Micropterus salmoides*, *M. dolomieu* Lacepede 1802, *Lymnaea columella* Say 1817, *O. mykiss*, *Lepomis macrochirus* Rafinesque 1819, *Physa acuta* Draparnaud 1805, *Tilapia sparrmanii* Smith 1840 and *O. mossambicus*) can all be regarded as "invasive" species, with the possible exception of *O. mykiss* which is regularly stocked in many catchments (Tables 8 and 9). Information on the abundance of species is incomplete and species have only been recorded as being "widespread" when sufficient information is available. Certain species, such as three of the fish parasites (*Trichodina acuta* Lom 1961, *Argulus japonicus* Thiele 1900 and *Ichthyophthirius multifiliis* Fouquet 1876), are likely to have a far wider distribution than those recorded in Tables 1 - 4. Other species (e.g. *P. clarkii*, *B. acheilognathi* and *Clarias gariepinus* (Burchell 1822)) have been introduced into new catchments within the past 20 years and have not yet had the opportunity to invade many catchments but are likely to be invasive species.

Among the fishes, the most widespread species include members of many reproductive guild categories, i.e. non-guarders (e.g. *C. carpio*), guardians (e.g. *T. sparrmanii*, *L. macrochirus* and *M. salmoides*) and external bearers (*O. mossambicus*). This supports Bruton's (1986) observation that it is not only the altricial species which become invasive. A closer analysis of distribution records of "widespread" species (Tables 1 - 4) indicates that *C. carpio* (a more "altricial" species) and *M. salmoides* (a more "precocial" species) do not conform to the expected distribution patterns (discussed in the introductory section) proposed by Bruton (1986). Both of these species are widespread in a number of relatively species-poor catchments. In some cases (such as in catchments G, U, Y2 and Z) both species are widespread within the same catchments. In other cases, there are differences in the distribution patterns but these can usually be ascribed to differences in habitat requirements. For example, *C. carpio* is widespread in certain turbid rivers such as the Vaal/Orange and the Fish River (catchments C, D and Q) whereas *M. salmoides* is rare in these systems (Tables 1 and 3). *M. salmoides* is widespread in the Olifants system (catchment E) where *C. carpio* has not been recorded. All of these rivers are relatively species-poor with respect to fish. On the other hand, neither carp nor bass have been successful in invading certain relatively species-rich catchments such as the Phongolo (W1) and northern Zululand (W2) (Tables 1 and 3) or in the more diverse lowveld regions of the Incomati (X) and Limpopo systems (lower A3) (van der Waal, pers. comm.). *M. salmoides* has, however, been more successful than *C. carpio* in invading the upper Incomati system (Table 3), which

Table 8. The degree of invasion of alien species in different catchments and sub-catchments.

Species	No. catchments invaded		No. sub-catchments in which the species is widespread
	s-c	m-c	
Total catchment number	41	24	
<i>Cyprinus carpio</i>	32	22	12
<i>Micropterus salmoides</i>	32	21	9
<i>Lymnaea columella</i>	24	16	9
<i>Oncorhynchus mykiss</i>	23	16	3
<i>Lepomis macrochirus</i>	19	16	6
<i>Micropterus dolomieu</i>	17	15	5
<i>Salmo trutta</i>	13	11	-
<i>Micropterus punctulatus</i>	8	8	-
<i>Physa acuta</i>	8	7	5
<i>Carassius auratus</i>	8	7	-
<i>Ctenopharyngodon idellus</i>	6	5	-
<i>Ichthyophthirius multifiliis</i>	6	5	-
<i>Gambusia affinis</i>	5	5	-
<i>Poecilia reticulata</i>	5	5	-
<i>Bothriocephalus acheilognathi</i>	5	4	-
<i>Trichodina acuta</i>	6	4	-
<i>Perca fluviatilis</i>	4	4	-
<i>Argulus japonicus</i>	4	3	-
<i>Tinca tinca</i>	3	3	-
<i>Xiphophorus helleri</i>	3	3	-
<i>Trachemys scripta</i>	2	2	-
<i>Hypophthalmichthys molitrix</i>	1	1	-
<i>Craspedacusta sowerbyi</i>	1	1	-
<i>Procambarus clarkii</i>	1	1	-

s-c = sub-catchment

m-c = major catchment

- = information not available

lends some support to Bruton's (1986) hypothesis. In order to further test this hypothesis, more records of the distribution and abundance of all the species mentioned (i.e. *O. mykiss*, *C. carpio*, *C. gariepinus*, *T. sparrmanii*, *M. salmoides*, *L. macrochirus*, *O. mossambicus* and *P. reticulata*) would have to be obtained and analysed.

Table 9. The degree of invasion of translocated indigenous species. The number of catchments which are beyond the native range of each species is also given.

Species	No. catchments beyond native range*	No. catchments invaded	No. catch- ments where widespread
<i>Tilapia sparrmanii</i>	17	15	5
<i>Oreochromis mossambicus</i>	11	9	4
<i>Clarias gariepinus</i>	16	5	-
<i>Barbus aeneus</i>	22	5	-
<i>Labeo capensis</i>	22	2	-
<i>Serranochromis r. jallae</i>	23	2	-
<i>Tilapia r. swierstrae</i>	19	2	-
<i>Sandelia capensis</i>	18	2	-
<i>Barbus anoplus</i>	5	2	-
<i>Labeo umbratus</i>	17	2	-
<i>Chetia flaviventris</i>	23	1	-
<i>Oreochromis macrochir</i>	23	1	-

* Information on native range obtained from Skelton (1993)

- = information not available

Future introductions

INTERBASIN TRANSFERS (IBTs)

There are at present seven completed interbasin transfer schemes in southern Africa (Pettijean and Davies, 1988), and five of these cross major catchment boundaries. A further six such schemes are either proposed or under construction in southern Africa (Pettijean and Davies, 1988) (Appendix 5). Although many hazards are encountered in most IBT's, certain species are able to survive such hazards. For example, in order to survive the journey from Teebus (Orange River) to the Grassridge Dam (Fish River), fish (or their eggs) have to pass through grids of 6.5 cm width, baffles and pepper-pot valves, as well as high pressures within the take-off chamber (Pettijean and Davies, 1988). Despite this, seven species of Orange River fish survived the passage through the Orange-Fish tunnel and have been recorded in the Fish River. Of these, *Labeo capensis* and *Clarias gariepinus*, which were previously not present in the Fish River, have established breeding populations (Cambray and Jubb, 1977 a and b; Laurenson and Hocutt, 1986). This case illustrates the likelihood of future translocations (via IBT's) into a number of major catchments (see Appendix 5).

Following the completion of the Vaal-Tugela scheme, three Vaal River species (*Barbus aeneus*, *Labeo capensis* and *L. umbratus*) were recorded in Kilburn Dam (Tugela system) (Coke, pers. comm.). The two former species appear to have established populations in the recipient river system (Coke, pers. comm.).

Skelton and Merron (1984) have completed a survey of the ichthyofauna in the donor (Okavango) and recipient rivers (Swakop and Omatako) of the Eastern National Water Carrier scheme (Appendix 5) which is still under construction in Namibia. Sixty-two species were recorded in the Okavango

River whereas only five species were recorded in the von Bach Dam (Swakop system) and Omatako Dam (Omatako River). It was considered that most of the Okavango River species would be unlikely to survive in the recipient system. There were, however, twenty species with broader ecological tolerances which they considered might not survive well in the canals and pipelines but could populate the various systems along the route of the carrier.

POSSIBLE FUTURE INTRODUCTIONS INTO THE OKAVANGO REGION

The widespread presence of three highly invasive alien species (*C. carpio*, *M. salmoides* and *O. mossambicus*) in small farm impoundments in the arid Omatako-Omarumba region (catchment Y1) in Namibia (Schrader, 1985; de Moor and Bruton, 1988), raises the possibility that these species may find their way into the Okavango system in the future. During normal flow rates the water bodies in the Omatako region are not connected to the Okavango system. In the event of rare flash floods these rivers flow into the Okavango River providing the opportunity for these species to reach the Okavango Swamps (Schrader, 1985). Water temperatures in the Okavango region range from approximately 18 - 29°C (Reavell, 1980). This is within the tolerance range of the three species mentioned above (de Moor and Bruton, 1988) so it is probable that they will be able to survive in the region. The possible negative impacts of invasions by these species into the Okavango Swamps area are described below.

Cyprinus carpio. Some workers have noted that this species uproots submerged vegetation (Crivelli, 1983) and disturbs bottom sediments. This has the overall effect of increasing the turbidity in the water. The altered environment then becomes less suitable for indigenous species (McCrimmon, 1968; Welcomme, 1984). There is, however, some dispute about the role of carp in causing these effects. Fletcher et al. (1985) found that there was no association between high carp densities and turbidity. They did however conclude that the presence of carp could cause a reduction in shallow-rooted, soft-leaved aquatic vegetation. Should carp succeed in establishing breeding populations in the Okavango, it could cause widespread ecological problems associated with the disturbance of bottom sediments.

Oreochromis mossambicus. This species could hybridise with indigenous cichlid species such as *O. andersonii* and *O. macrochir* (Boulenger 1912) in the Okavango region (Skelton, pers. comm.). Such genetic contamination could decrease the biological fitness of indigenous fish stocks (Welcomme, 1988).

Micropterus salmoides. This is a predatory species that has had major negative impacts in isolated river systems in the southern Cape, which have a high degree of endemism. Since a number of voracious indigenous predators (such as the tigerfish, *Hydrocynus vittatus* Castelnau 1861 and the African pike, *Hepsetus odoe* (Bloch 1794)) occur in the Okavango (Skelton et al., 1985), indigenous species may not be so vulnerable to predation as was the case in the Cape rivers, where no large specialist indigenous predatory species occurred prior to the introduction of trout and bass.

It is difficult to predict with certainty whether the three alien species mentioned above would be successful in establishing populations in the Okavango which is a diverse ecosystem with approximately 80 species of fish (Skelton et al., 1985). Given the evidence that carp and bass have not succeeded in invading species-rich catchments in the eastern Transvaal lowveld, it seems unlikely that these species will succeed in the species-rich Okavango system so long as the condition of this system remains in a relatively pristine state. *O. mossambicus*, a "tropical" species with a precocial life-history style, seems more likely to succeed in invading the Okavango.

The Okavango system, although still relatively pristine compared to many rivers in southern Africa, has been subjected to some major disturbances such as water abstraction, poor catchment

management, insecticide spraying, and channelisation (Skelton et al., 1985; Merron and Bruton, 1990). Fox and Fox (1986) found a direct correlation between the degree of disturbance and the susceptibility of a biotope to invasion by alien species. An increase in the levels of disturbance is therefore likely to increase the vulnerability of the Okavango region to invasion. For this reason, it would be unwise to adopt a complacent attitude towards the potential of alien species to invade the system.

Conclusion

Invasive aquatic animals disrupt ecological processes, threaten the genetic integrity of indigenous species, and alienate aquatic habitats. They therefore constitute a severe threat to aquatic ecosystems and need to be monitored and controlled. Distribution records of alien species are not complete, but these do indicate that the problem has reached alarming proportions. The threat posed by invasive species needs to receive as much attention in South Africa as water pollution and habitat deterioration because it contributes to both and causes additional negative repercussions. The importation and translocation of invasive species needs to be strictly controlled and quantitative studies need to be carried out on the impacts of widespread invasive species. It is recommended that special measures be taken to minimise the possibility of the introduction of alien species into certain waterbodies of high conservation status (the Okavango, Mkuze Swamps and Lake Sibaya) which have not as yet been invaded by alien fish. It is noted that these waterbodies are in tropical or sub-tropical regions where water temperatures are likely to be within the tolerance range of many species associated with the aquarium trade.

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APPENDIX 1

Major catchments and sub-catchments in the study area (illustrated in Fig. 1) as well as the major rivers, impoundments and towns in each region. DWA sub-catchments also listed where such information is available*.

Region	Major Rivers & tributaries	Major waterbodies/impoundments	Towns/places
<u>A - Limpopo</u>			
A1	-Crocodile, Jukskei, Marico (A10,A20,A30)	Rietvlei Dam, Hartbeespoort Dam, Roodeplaat Dam, Marico-Bosveld Dam	N-Johannesburg, Pretoria
A2	Botswana tributaries: -Lotsani, Shashi, Metsemothlaba	Shashi Dam Gaberone Dam	Gaberone
A3	-Levuvhu (A40,A50,A60,A70,A80,A90)	Nzhelele Dam, Albasina Dam, Glen Alpine Dam, Hans Strydom Dam	Pietersburg, Potgietersrus

Appendix 1. Continued.

Region	Major Rivers & tributaries	Major waterbodies/impoundments	Towns/places
<u>B - Olifants</u>			
B1	-Blyde, Treur, Steelpoort (B10,B20,B40,B60)	Bronkhorstspuit Dam, Blyderivierspoort Dam	Bronkhorstspuit
B2	-Elands (B30,B50)	Rust de Winter, Loskop Dam	Marble Hall, Witbank
B3	-Letaba (B70,B80,B90)	Fanie Botha Dam, Ebenezzer Dam	
<u>C - Vaal</u>			
C1	-Klip, Wilge (C10,C80)	Grootdraai Dam, Sterkfontein Dam	Bethlehem, Standerton
C2	-Skoonspruit, Vet, Mooi, Vals (C20,C40,C60,C70)	Allemanakraal Dam, Boskop Dam Erfenis Dam, Vaal Dam	S. Johannesburg, Klerksdorp, Parys, Potchefstroom,
C3	-Hartz, Modder, Riet (C30,C50,C90)	Barberspan, Bloemhof Dam, Kalk- fontein Dam, Spitzkop Dam	Bloemfontein, Kimberley
<u>D - Orange</u>			
D1	- Malibamatso, Mokhotlong, Senqu		Lesotho highlands
D2	-Caledon, Kraai, Makeleng (D10,D20)		Maseru
D3	-Seekoei (D30,D60,D70)	PK le Roux Dam, Verwoerd Dam	Douglas, Upington
D4	-Hartbees, Sak (D50)	Rooidam	
D5	-Kuruman, Malopo (D40)	Kuruman Oog, Malopo Oog	Kuruman
D6	-Fish (D80+Fish R.)	Hardap Dam	Oranjemond
E	Olifants (Clanwilliam) - Tankwa, Doring, Twee, Driehoek	Bulshoek Dam, Clanwilliam Dam	Clanwilliam
F	Buffalo, Swartdoring		
G	Berg, Bot, Eerste, Heuningnes, Klein, Palmiet	Paardevlei, Princessvlei, Seekoeivlei	Cape Town, Somerset W., Stellenbosch
H	Breede - Hex, Nuy, Riviersonderend	Brandvlei Dam, Theewaterskloof	Riviersonderend
J	Gouritz - Gamka, Groot, Touwsrivier	Gamkapoort Dam	Oudtshoorn
K	South coastal Keurbooms, Kromme, Tsitsikama,	Groenvlei, Rondevlei, Swartvlei	Knysna, Plettenberg Bay
L	Gamtoos - Baviaanskloof, Groot, Wit	Paul Sauer Dam	Patensie
M	Baakens, Swartkops,		Port Elizabeth, Uitenhage
N	Sundays	de Hoop Dam, Lake Mentz,	Kirkwood
P	Bushmans, Kariega, Kowie	Howiesonspoort Dam	Grahamstown, Port Alfred

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Appendix 1. Continued.

Region	Major Rivers & tributaries	Major waterbodies/impoundments	Towns/places
Q	Fish	Grassridge Dam, Lake Arthur	Cradock
R	Buffalo, Keiskamma, Nahoon	Bridle drift Dam, Maden Dam, Rooikrans Dam	East London, Kingwilliamstown
S	Kei - Kubusie, Swart Kei	Gubu Dam, Lubisi Dam, Nqora Dam, Xonxa Dam,	Stutterheim
<u>T - S. Natal/Transkei</u>			
T1	Mngazi to Kobongaba: Mbashe Mngazi, Mtata (T10,T20,T70,T80)	Mtata Dam	Umtata
T2	Mzamba to Mzimvubu (T30,T60) Mzimvubu - Mzimhlava, Tina, Tinana		Mount Frere, Kokstad Port St. Johns
T3	Mzimkulu (T40,T50) - Pholela, Mzimkulwana, Mtamvuna, - Ngwangwana		Harding, Margate
U	Mgeni - Karkloof, Msindusi, Mkomazi - Mquatsheni, Loteni	Albert Falls Dam, Midmar Dam, Nagle Dam	Durban, Pietermaritzburg
V	Tugela - Buffalo, Mooi	Chelmsford Dam, Spionkop Dam, Wagendrift Dam, Woodstock Dam	Estcourt, Newcastle
<u>W - Zululand/Swaziland</u>			
W1	Ngwavuma, Phongolo, Usuthu (W40,W50,W60)	Jericho Dam, Kosi Bay, Pongolapoort Dam, Westoe Dam	Mbabane Pongola
W2	Mfolozi, Mhlatuze, Mkuze, (W10,W20,W30,W70)	Mkuze Swamps, Lake Sibaya	Richards Bay
<u>X - Nkomati</u>			
X1	Sabie (X30,X40)		Sabie
X2	Crocodile (X20)		Nelspruit
X3	Komati, Mbuluzi (X10)	Kafferskraal, Nooitgedacht	N. Swaziland
<u>Y - Botswana/Namibia</u>			
Y1	Chobe, Okavango	Makgadikgadi Pans, Okavango Swamps	Maun
Y2	Omatika Omarumba		
Z	Swakop, Kuiseb	von Bach Dam, Kuiseb Canyon	Windhoek, Swakopmund

- Indicates major tributaries of river indicated.

* Code for sub-catchments according to Department of Water Affairs statistics (Anon, 1986).

APPENDIX 2

Checklist of alien species introduced into southern Africa together with selected bibliography (in numerical and alphabetical code, listed in Appendix 4).

Scientific classification and common name	Native range	Date of first introduction	Impact ¹	Distribution references
Ciliophora Ichthyophthiriidae <i>Ichthyophthirius multifiliis</i> Fouquet 1876 whitespot, ich	Possibly Asia (78)	Uncertain (78)	PF (116) major	116,149, 1
Oligohymenophorea <i>Trichodina acuta</i> Lom 1961 trichodina	Uncertain (116)	Possibly 18th C. (c)	PF (116) major	14, 149
Cnidaria Limnomedusae <i>Craspedacusta sowerbyi</i> Lankester 1880 Freshwater medusa	N. hemi- sphere (129)	late 1970's (130)	LI (129, 130)	130
Platyhelminthes Bothriocephalidae <i>Bothriocephalus</i> <i>acheilognathi</i> Yamaguthi 1934 fish tape worm	Asia (78)	1975 (25)	PF (25) major	18,25,148
Arthropoda Crustacea Argulidae <i>Argulus japonicus</i> Thiele 1900 fish louse	Possibly Asia (78)	Prior to 1983 (104)	PF (104) major	104,149, 1
Parastacidae <i>Cherax tenuimanus</i> (Smith 1912) marron	SW Australia	c. 1982 (23) (112)	LI (160)	160, r
Cambaridae <i>Procambarus clarkii</i> (Girard 1852) red swamp crayfish	N. America (134)	c. 1992 (134)	Possibly HD (134)	134
Mollusca Physidae	Probably N. America	c. 1966 (57,151)	LI	27,57,128,154

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Appendix 2. Continued.

Scientific classification and common name	Native range	Date of first introduction	Impact ¹	Distribution references
<i>Physa acuta</i> Draparnaud 1805 physa snail	26			
Planorbidae <i>Helisoma duryi</i> Weatherby 1879 helisoma snail	N. America (b)	c. 1969 (b)	LI (11)	11
Lymnaeidae <i>Lymnaea columella</i> Say 1817 lymnaea snail	N. America (b)	c. 1944 (28)	VPL 27,28 major	29,115,127,128, 133,150,153,154
Chordata Osteichthys Salmonidae <i>Oncorhynchus mykiss</i> (Walbaum 1792) rainbow trout	Western N. America & E. Asia (108,145)	c.1897 (2,43,46, 64,71,76)	P major in some cases (36,103)	39,40,41,42,45,47, 50,54,62,70,87, 108,123,139 a,e,g,h,i,j,k,l, m,n,o,p,x,y,z 1000, 2000
<i>Salmo trutta</i> Linnaeus 1758 brown trout	Europe, W. Asia & Morocco (161,j)	Late 19th C. (2,6, 119)	P (140) major in some cases (123)	40,41,50,54,65,66, 67,69,75,80,81,94, 131,140,155 h,k,t,y 1000, 2000
Cyprinidae <i>Carassius auratus</i> (Linnaeus 1758) goldfish	E.Europe, central Asia & China (163)	c. 1728 (142)	IP 78	39,40,60,72,77, 100, p 1000, 2000
<i>Ctenopharyngodon idellus</i> (Valenciennes 1844) grass carp	Asia (83)	1967 (23)	DAV, IP (25,120,122)	p
<i>Cyprinus carpio</i> Linnaeus 1758 common carp	Asia & E. Europe (12,85)	18th century (4,142)	IP, DAV, HD (2,78,85, 109,162, 164,165)	3,5,9,15,17,24, 31,35,36,40,44,47, 51,56,58,62,74,75, 77,81,95,100,101, 103,105,106,109,118, 124,132,139,143, i,q,s,w,y,aa 1000, 2000
<i>Hypophthalmichthys molitrix</i> (Valenciennes 1844) silver carp	China & E. Siberia (163)	1975 (163)	unknown	1 2000

Appendix 2. Continued.

Scientific classification and common name	Native range	Date of first introduction	Impact ¹	Distribution references
<i>Tinca tinca</i> Linnaeus 1758 tench	Europe & W. Asia (162)	1910 (2)	LI	8,24,97, o,w
Poeciliidae <i>Gambusia affinis</i> (Baird & Girard 1854) gambusia, mosquitofish	SE & central N. America (108)	1936 (2)	C	152, l,p,u
<i>Poecilia reticulata</i> (Peters 1859) guppy	S. America north of Amazon R. (82)	1912 (61,136)	C,	f,v,w 1000,2000
<i>Xiphophorus helleri</i> Heckel 1840 swordtail	S. Mexico & Guatemala (146)	Before 1974 (7,96)	C, PFL (96)	10 w,x 1000,2000
Centrarchidae <i>Lepomis macrochirus</i> Rafinesque 1819 bluegill sunfish	E & central N. America (135)	1938 (61)	C, PFL major (49,85, 87)	20,22,35,39,40,50, 58,81,94,111,139, 152,155, d,l,y,aa, 1000
<i>Micropterus dolomieu</i> Lacepede 1802 smallmouth bass	E. Canada & USA (108)	1937 (63)	P major (9,35,49, 102,126, 140)	24,39,80,87,93,98, 101,102,126,159 e,k,y,ab 1000,2000
<i>Micropterus punctulatus</i> (Rafinesque 1819) spotted bass	SE of USA (108)	1939 (68)	unknown	e,g,m 1000,2000
<i>Micropterus salmoides</i> (Lacepede 1802) largemouth bass	N. America (135)	1928 (2)	P major 2,13,23, 35,87,140	13,15,21,37,40, 44,47,53,58,73,75,80, 81,84,90,94,113,132, 139,143,144,152,157, e,g,h,y,z,aa,ab 1000,2000
Percidae <i>Perca fluviatilis</i> Linnaeus 1758 perch	Europe & Asia (79)	1927 (2)	LI (23)	p 1000
Cichlidae <i>Oreochromis aureus</i>	Middle E & NE Africa	c. 1965 (157)	LI PH	157

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Appendix 2. Continued.

Scientific classification and common name	Native range	Date of first intro.	Impact ¹	Distribution References
(Steindachner 1864) Israeli tilapia	(147)		(31)	
<i>Oreochromis niloticus</i> (Linnaeus 1758) Nile tilapia	Middle E. & NE Africa (147)	c. 1959 (156)	LI PH (156)	156
Reptilia Testudinae <i>Trachemys scripta elegans</i> (Schoepff 1792) red-eared terrapin	SE of USA (38)	Before 1984 (114)	Poss. VPM (114)	114

Legend for impact of species.

C - Competition with indigenous species

DAV - Destruction of aquatic vegetation

HD - Habitat destruction

IP - Associated with the introduction of parasites

PH - Possibility of hybridisation with congeneric indigenous species

LI - Little impact

P - Predator of indigenous species

PF - Parasite of indigenous fish

PFL - Predator of fish larvae and eggs

VPL - Vector of parasites of livestock

Major - Indicates major impact of species on the aquatic environment

APPENDIX 3

Checklist of translocated indigenous species whose native range is within the study area together with selected bibliography (in numerical and alphabetical code, listed in Appendix 4).

Scientific classification and common name	Catchments* of native range	Impact ¹	Distribution references
Cyprinidae <i>Barbus aeneus</i> (Burchell 1822) smallmouth yellowfish	C,D (141)	uncertain, PH (107)	32,33,34,86,89, 92,107,137, e.i, 1000
<i>Barbus anoplus</i> Weber 1897 chubbyhead barb	A1,B1,C,D1,D2, D3,D4,D5,E,J, L,M,P,Q,R,S,T3 ² U ³ ,V,W,X (141)	uncertain	1,44

Appendix 3. Continued.

Scientific classification and common name	Catchments* of native range	Impact ¹	Distribution references
<i>Labeo capensis</i> (Smith 1841) Orange River labeo	C,D (141)	C,PH	32,33,34,48,i, 1000
<i>Labeo umbratus</i> (Smith 1841) mud mullet	C,D,J,L,N,P,Q (141)	HD (88)	32,87,88,90, 141,i, 1000, 2000
Clariidae <i>Clarias gariepinus</i> (Burchell 1822) sharptooth catfish	A,B,C,D,V,W,X,Y (141)	P,C expect major impact (107,110)	33,34,52,107, 110, 1000,2000
Cichlidae <i>Chetia flaviveutris</i> Trewavas 1961	A (141)	uncertain	1
<i>Oreochromis andersouii</i> (Castelnau 1861) three spot tilapia	Y (117,141)	PH	55
<i>Oreochromis macrochir</i> (Boulenger 1912) greenhead tilapia	Y (141)	PH	55,1
<i>Oreochromis mossambicus</i> (Peters 1851) Mozambique tilapia	A,B,P,Q,R,S,T, U,V,W,X (141)	C,PH, expect major impact (41,52,132)	17,41,44,51,91, 132,138,141,158 1000
<i>Sargochromis codringtoni</i> (Boulenger 1908) green happy	Y (117)	PH	55
<i>Serranochromis angusticeps</i> (Boulenger 1907) thinface largemouth	Y (141)	PH	55
<i>Serranochromis robustus</i> (Boulenger 1896) nembwe	Y (141)	PH	55,119,121, s
<i>Serranochromis thumbergi</i> (Castelnau 1861) brownspot largemouth	Y (141)	PH	55
<i>Tilapia reudalli</i> Gilchrist & Thompson 1917 redbreast tilapia	A,B,W,X,Y (141)	DAV major impact (16,99,125)	19,30,119,122,125 1000,2000

Appendix 3. Continued.

Scientific classification and common name	Catchments* of native range	Impact ¹	Distribution References
<i>Tilapia sparrmanii</i> Smith 1840 banded tilapia	A,B,C,D3,D4,D5, D6,W,X,Y (141)	C (49,140)	24,35,50,74,87, 140,155,1000,2000
Anabantidae <i>Sandelia capensis</i> (Cuvier 1831) Cape rocky	G,H,J,K,L,M (141)	C (59)	59,x,1000

* Ref. Fig. 1 & Appendix 1 for codes and description of catchments

1 Legend for the impact of species as in Appendix 2

2 Although the native range includes most of the T and U catchments (Skelton 1993), *Barbus anoplus* is absent from the Mkomazi and Mzimkulu catchments within U and T₃ respectively.
Although normally translocations within major catchments are beyond the scope of this paper, an exception is made here since these catchments are completely separated from others within the major catchments of U and T₃.

APPENDIX 4

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Museum records

1000 - Albany Museum record.

2000 - J.L.B. Smith Institute of Ichthyology record.

APPENDIX 5

Existing and future interbasin transfer schemes between major catchments in southern Africa which could result in further translocations (after Pettijean and Davies, 1988).

Scheme	Status	Donor catchment	Recipient river(s) & catchment
Usuthu-Vaal	Completed	Vaal (C1) Usuthu (W1)	Steenkoolspruit Olifants (B1) Vaal (C1)
Tugela-Vaal	Completed	Tugela (V)	Vaal (C1)
Orange project	Sections completed	Orange (D3) Fish (Q)	Fish (Q) Sundays (N)
Riviersonderend-Berg	Completed	Breede (H)	Eerste (G)

Appendix 5. Continued.

Scheme	Status	Donor catchment	Recipient river(s) & catchment
Eastern National Water Carrier	Under construction	Kavango (Y2)	Swakop (Z)
Lesotho Highlands	Under construction	Upper Orange (D1)	Vaal (C2)
Amatola	Under construction	Toise & Kubusie Kei (S)	Nahoon & Yellowwoods (R)
Mooi-Mgeni	Under construction	Mooi (Tugela) (V)	Mpofana (Mgeni) (U)
Mzimkulu-Mkomazi	Under construction	Mkomazi (U) Mzimkulu (T3)	Mgeni & Illovo (U) Mkomazi (U)
Zambezi aqueduct	Proposed	Zambezi	Botswana & Vaal (Y1, D5, C3)

Addendum

At the time of going to press the following two new distribution records were received:

Gambusia affinis in the Fish River (catchment Q) (Ter Morshuizen pers. comm.)

Oreochromis mossambicus in the Gouritz catchment (J) (Bok pers. comm.)

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**Nesting and flower visiting of some southern African Anthophorini
(Hymenoptera: Apoidea: Apidae: Apinae)**

F.W. GESS and S.K. GESS

Published jointly by the Cape Provincial Museums
at the Albany Museum, Grahamstown, South Africa

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Nesting and flower visiting of some southern African Anthophorini (Hymenoptera: Apoidea: Apidae: Apinae)

by

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ABSTRACT

Accounts are given of nesting in horizontal or gently sloping ground by two species of *Amegilla* Friese, *A. (Micramegilla) atrocincta* (Lepeletier) and *A. (Zebramegilla) punctifrons* (Walker). The burrow of *A. (M.) atrocincta* is excavated using water and the entrance is surmounted by a turret. Each shaft, of which there may be more than one per nest, is terminated by a single cell. Water is not used in excavation by *A. (Z.) punctifrons*. Soil particles are extracted using the mandibles and are raked out of the burrow. Each shaft, of which there may be more than one per nest, is terminated by several cells in linear series. Notes are given on the nesting in vertical earthen banks by two species of *Anthophora* Latreille, *A. (Heliophila) praecox* Friese and *A. (Paramegilla) epichariformis* Gribodo neither of which constructs an entrance turret.

Evidence is given for possible associations between *Thyreus alfkeni* Brauns and *Thyreus delumbatus* (Vachal) and *A. (Z.) punctifrons*, and between *Thyreus calceatus* (Vachal) and *A. (H.) praecox*.

Flower visiting records, totalling 502, are given for 16 species of *Amegilla* and 10 species of *Anthophora*. Analysis of these records shows that the differences in flower choice between genera and also between subgenera (despite the lack of distinction between pollen and nectar collection) indicate that the Anthophorini do not as a rule practise indiscriminate broad polylecty.

INTRODUCTION

Remarkably little has been published on the biology of the southern African species of *Anthophora* Latreille and *Amegilla* Friese (Apoidea: Apidae: Apinae: Anthophorini). Brauns (1913) and Rozen (1969) gave life history notes on two species of *Anthophora*. Although some observations were made by the present authors from time to time over the past twenty years the difficulty experienced in determining the voucher specimens discouraged more intensive investigation. With the recent taxonomic revisions of the southern African species of these genera (Eardley and Brooks 1989, Eardley 1994) the identification of these bees has been greatly facilitated. It seems useful to present and discuss the available nesting observations and flower visiting records despite the fact that on the whole they are of a somewhat fragmentary nature. This may lay the foundation and provide the stimulus for further investigations.

NESTING

Amegilla (Micramegilla) atrocincta (Lepeletier)

Geographic distribution

Amegilla (Micramegilla) atrocincta occurs throughout southern Africa, with the noticeable exception of the region incorporating southern Namibia, and the northern, central and western Cape Province (Eardley 1994).

Nesting areas, nesting sites and nesting density

Two nesting areas have been located on the farms Hilton (27.15S, 32.21E) and Clifton (27.11S, 32.24E), respectively 18 and 19 kilometres WNW Grahamstown in the southeastern extension of the Nama Karoo. The vegetation of Clifton, the more easterly farm, differs from that of Hilton in having a higher succulent element. The nesting sites were in bare areas of non-friable clayey soil in low scrub, all in close proximity to water. The surface of the ground chosen for nesting was in all instances horizontal to subhorizontal.

During the eight years from 1973 to 1981 during which the authors were working intensively on the farm Hilton *Amegilla atrocineta* was very rarely sighted. Only two single nests were found, one in 1973 and one in 1978.

In some years *Amegilla atrocineta* has been relatively commonly encountered on forage plants at Clifton; however, the nests have proved difficult to locate. No aggregations of nests were found, only single widely scattered nests. During the summer 1985/1986, when a deliberate effort was made to locate nests, only five nests were found.

Brauns (1913) commented that, at Willowmore, he found *A. atrocineta* (as *Anthophora plunnipes*) nesting in areas of hard level ground, the nest entrance generally covered by a stone. No nests so sited have been found by the authors.

Flight period

Collecting dates (collected records from Eardley 1994, additional records from label data Albany Museum) throughout the range of *A. atrocineta* suggest that this bee is most commonly in flight from mid- to late-summer, December to March in the Cape Province. Certainly in the vicinity of Grahamstown, where the Gesses have collected throughout the year, this bee is most commonly encountered in January and February. To the north in the Transvaal, Zimbabwe and Namibia the flight period is more extended there being scattered records from September through to May.

Flower visiting

All plants in flower on Hilton and Clifton were sampled for flower visitors at intervals throughout the summer. It was found that males and females of *Amegilla atrocineta* commonly visited the white flowers of *Blepharis capensis* (L.f.) Pers. (Acanthaceae) at Clifton during January and February. An additional two males were taken on flowers of *B. capensis* at Waterford (33.07S, 25.01E). Though not sampled *A. atrocineta* was observed visiting the yellow flowers of *Cotyledon campanulata* Marloth (Crassulaceae) in addition to those of *B. capensis* during January 1986 when the nesting behaviour of the bees was being investigated on Clifton. No forage plants of these bees were located at Hilton. The only other flower visiting records available are of two females taken on the yellow flowers of *Berkheya heterophylla* (Th.) O.Hoffm. (Asteraceae) between Lynton and Vlakwater (27.09S, 32.18E). Voucher specimens are listed in Appendix 1 under Grahamstown and Waterford.

Provision

The provision is in the form of a syrup on which the egg or larva floats. Pollen from the cells of two nests at Clifton was examined microscopically. Though mixed, the bulk of the pollen from both nests matched that of *C. campanulata*. No pollen matching that of *B. capensis* was found suggesting that this plant was principally visited for nectar. However, provision from a third nest, investigated

when the flowers of *C. campanulata* were almost over, contained an appreciable proportion of pollen matching that from *B. capensis* and *Peristrophe cernua* Nees (Acanthaceae) but very little pollen matching that from *C. campanulata*.

The cells when opened gave off a marked odour which could be described as "meady" or "cheesy". It was probably a combination of odours derived from the provision and the waxy Dufour's gland secretion.

Male behaviour

At Clifton, in addition to feeding at the flowers of *B. capensis* males were frequently observed patrolling a patch of this plant growing in close proximity to nest sites. None was observed in the vicinity of nests.

Sheltering and sleeping

A nesting female was observed by the present authors sheltering head downwards in her nest. Males and un-mated, and therefore nestless, females were observed by Brauns (1913) spending the night on low plants, up to 10 bees in a row on a single twig, holding on firmly with their mandibles, and in smaller numbers under stones.

Description of nest

The nest consists of a subterranean burrow surmounted by a cylindrical erect or inclined turret constructed from mud and having an inner diameter of 9 mm and reaching lengths of up to 80 mm (Fig. 1). Individual applications of mud are visible on the outside of the turret but the inside is smoothed.

The burrows of six of the seven nests investigated consisted of a single subvertical shaft, 8-9 mm in diameter. Four terminated in a single cell and two had not reached the stage of cell construction. The burrow of the sixth nest bifurcated just below the surface of the ground (Fig. 2). One shaft, apparently the first excavated, led directly downwards whereas the other at first sloped gently before continuing downwards parallel with the first shaft. Each shaft terminated in a single cell at an average depth of 172.4 mm (sample of five, range 130-208 mm). The sides of the cells were parallel and the base was rounded. The diameter of the cells was the same or marginally greater than that of the shafts. The lengths of the two cells measured were 20 and 23 mm. The walls were smooth and lined with white wax. Each cell was closed with a mud and wax plug which was somewhat smoothed above but not below and which was slightly concave above and was either flat or somewhat concave below as the plug was sometimes deeper around its circumference than at its centre. Above each cell plug was a capping of mud. Above this a portion of shaft, slightly shorter than a cell, with smoothed walls formed a chamber. This chamber was full of mud pellets, and was sealed with a mud plate. The shaft above this chamber was full of loose earth and there was an additional mud plate at a variable height along its length. In one nest a mud plate sealed the shaft at ground level within the turret.

Method of construction

Water is required for the excavation of the burrow, construction of the turret, smoothing of the cell walls and construction of the mud seals. Water is collected by the female from a nearby pool. Whilst taking in water she stands on the mud at the water's edge.



Fig. 1. Nest entrance turret of *Amegilla* (*Micramegilla*) *atrocineta* (Lepeletier) on the farm Hilton (27.15S, 32.21E). Actual height of turret 45 mm.

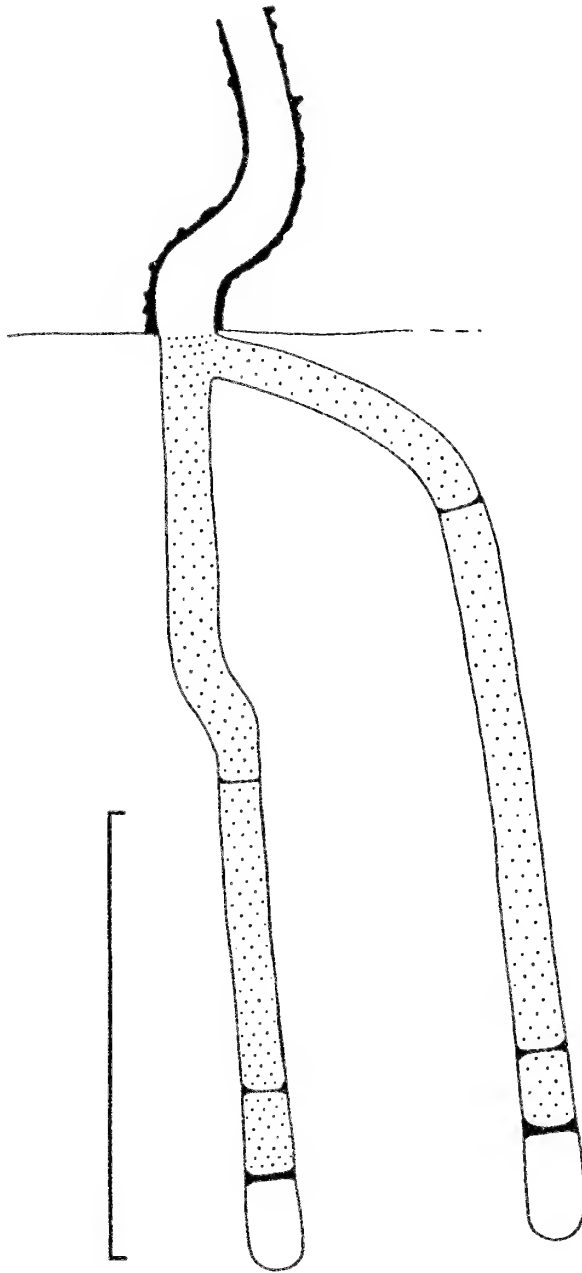


Fig. 2. Vertical plan of one of the nests of *Amegilla* (*Micramegilla*) *atrocineta* (Lepelletier) investigated on the farm Clifton (27.11S, 32.24E). Scale bar = 10 cm.

Having selected a suitable nesting site and returned with a load of water the female initiates excavation. She regurgitates the water and mixes it with the soil to form mud which she passes back beneath herself, rotating steadily. The mud is positioned around the rim of the shaft initial to form the base of the turret. Further extracted mud is passed back in the same manner and is positioned by the tip of the abdomen. The lengths of time spent away from the nest collecting water, actually imbibing water and working at the nest excavating mud and working on the construction of the nest were measured for one of the builders. She was found to take 20-34 seconds away from the nest to fetch water, 13-14 seconds to tank up, and for each water load 2-3 minutes excavating, adding two loads of mud to the turret and smoothing it on the inside. On her return flights to the nest she circled above the nest and then flew straight in.

In one instance a shaft passed through a patch of weakly structured soil. The walls of this section of the shaft had been shored up by cementing with mud.

The excavated cell walls were smoothed apparently with the use of water. There was no constructed mud cell within the excavated cell. The wax lining of the cell forms a distinct layer which can be separated from the earthen wall.

The wax coating of the cell wall extends into the mouth of the cell. The mud and wax plug sealing the cell is constructed within the mouth of the cell fitting like a stopper into the neck of a jar. The mud is laid down spirally; however, the spiral is not continuous as each load of mud is added without matching the end of the previous spiral which is little more than a ring with overlapping ends. Five such broken rings could be counted on one of the plugs. The central remaining aperture is crudely plugged with a final load of mud which may project on the lower surface as a rough knob. The manner in which the wax is applied is not clear. As the lower surface of the plug including the knob has a visible white coating it is thought that the wax is probably added with the mud. The upper surface is roughly smoothed and given a light wax coating. An additional mud capping is added above the stopper and this bonds with the walls of the shaft above the cell.

The mud capping added above the cell plug, unlike the plug shows no patterning. It is, apparently, simply a layer of mud spread over the plug and onto the walls at the base of the chamber above the cell. Its function appears to be to completely seal the cell, as the plug is not firmly attached to the cell walls there being a layer of wax between the earthen walls and the plug. No wax is added to this capping or to the walls of the chamber above the cell. The function of the wax appears to be to waterproof the cell, the provision being fluid.

Associated insects

Of the seven nests two were found to have been "parasitised".

One nest had been usurped by a megachilid. This nest contained one *A. atrocincta* cell which had been lined with wax and partly provisioned. The cell and the shaft above it had been filled with gravel to a height of 30 mm above the cell. The megachilid bee had then constructed a petal cell sealed above with a petal disc. The sealing disc was identified as being cut from a white petal of *B. capensis*. The remainder of the shaft had been filled with gravel. Pollen from the provision was examined and found to be of two forms, one of which matched that of *P. cernua* (Acanthaceae) and the other *Pentzia incana* (Thunb.) Kuntze (Asteraceae).

In the other nest eight non-phoretic triungulin larvae of a meloid beetle were found in the single sealed cell.

Amegilla (Zebramegilla) punctifrons (Walker)

Geographic distribution

Amegilla (Zebramegilla) punctifrons is widespread in subsaharan Africa, and apparently occurs throughout the subcontinent, except that it is noticeably absent from the western, southwestern, central and northern Cape Province, and from the southern half of Namibia (Eardley 1994).

Nesting areas, nesting sites and nesting density

Brauns (1913) noted that *A. (Z.) punctifrons* (as *Anthophora circulata*) nests in extensive aggregations in bare level places in the vicinity of Willowmore. The present authors have located two further nesting areas. One in the eastern Nama Karoo on the neighbouring farms of Clifton (27.11S, 32.24E) and Thursford, WNW of Grahamstown, and the other in the southern Great Karoo at the interface between the Succulent Karoo and the Nama Karoo on the farm Tierberg (33.08S, 22.16E), to the east of Prince Albert. The sites of nesting aggregations in these areas are bare patches of horizontal to gently sloping clayey ground in karroid scrub with a strong succulent element. In all instances, although there was an abundance of similar bare areas and although the bare areas selected were extensive, even in small aggregations, the nests were crowded together, new nests being added around the fringes of the aggregations.

Flight period

Collecting dates (collected records from Eardley 1994 and additional records from Albany Museum) suggest that *A. (Z.) punctifrons* is in flight in the southern and eastern Cape from early summer, October, through to late summer, March. To the north in the northern Transvaal and Zimbabwe it is possible that it flies through the winter as it has been collected from June to August.

Flower visiting

On the farm Clifton females and males of *A. (Z.) punctifrons* regularly forage together with *A. (M.) atrocincta* on the white flowers of *Blepharis capensis* (Acanthaceae) in January and February. In addition in October early flying males were taken on the same flowers at Clifton and on yellowish-white flowers of a "mesem" (Mesembryanthemaceae) on Verdun (33.10S, 25.50E) in the Kommadagga District to the north west of Clifton. Voucher specimens are listed under Grahamstown and Kommadagga in Appendix 1.

No forage plants of *A. (Z.) punctifrons* were located on Tierberg.

Provision

Provision from the cells of nests excavated on Tierberg was a very wet mixture of pollen and nectar. Some of the pollen was examined microscopically and was found to be of two types, one relatively large and oval and the other relatively small and spherical, both smooth walled as seen with the light microscope. Though comparisons with pollen from plants in flower were made it was not possible to identify the pollen with any certainty.

Sheltering and sleeping

Sleeping by *A. (Z.) punctifrons* has not been observed by the present authors but has been recorded at Willowmore by Brauns (1913). He found sleeping clusters of males and females mixed, up to 30, on low bushes, the bees being firmly clamped onto the stems by means of their mandibles. More rarely, males were found sheltering together with males of *Amegilla niveata* (Friese) (as *Anthophora niveata*) in hollow stems, lying on the ground, and in dry open seed capsules of *Datura*. Actively nesting females appeared to retire to their nests at night.

Description of the nest

Access to all nests was direct. In no instance was there any form of nest entrance turret. Three nests of a nesting aggregation on Tierberg were excavated. The shaft, 6- 6.5 mm in diameter, in all three nests initially sloped gently downwards before continuing subvertically at a constant diameter to a depth of 95-105 mm below which it ended in one to three subvertical to sloping cells in linear series (Fig. 3). In two of the nests there were secondary shafts in addition to the main shaft, in one a single secondary shaft and in the other two and the initial of a third. The secondary shafts in turn each

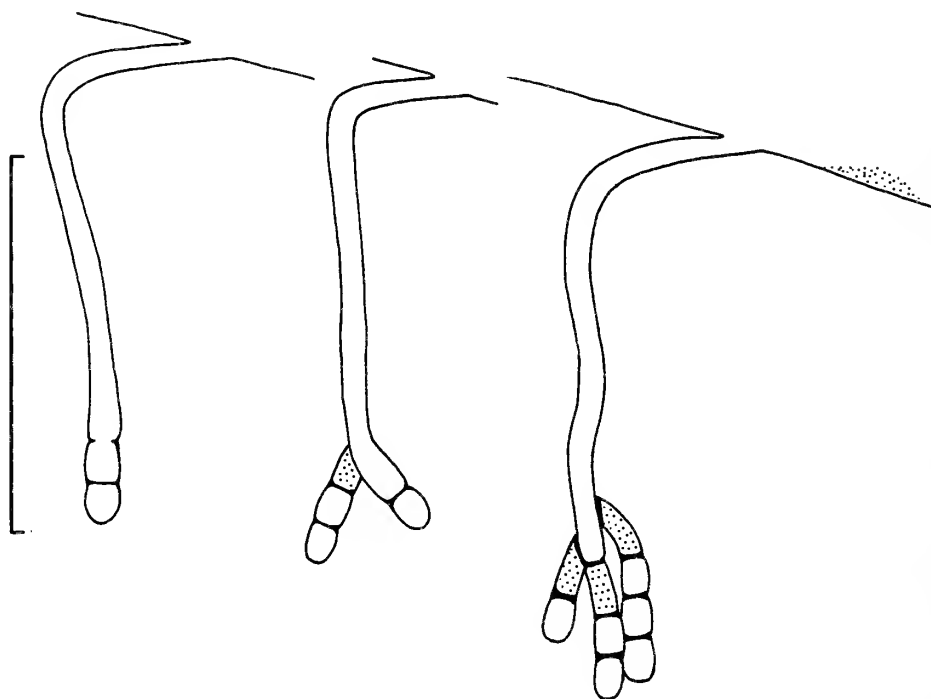


Fig. 3. Vertical plans of the nests of *Amegilla (Zebamegilla) punctifrons* (Walker) investigated on the farm Tierberg (33.08S, 22.16E). Scale bar = 10 cm.

ended in a linear series of cells. Between the last completed cell in each series and the opening to the next excavated shaft the shaft had been filled with earth and sealed off from the main shaft with a mud-plate. Twelve cells in all were obtained. Each was 10 mm long and 7-7.5 mm in diameter at mid-length. The walls were cemented and smoothed, and coated with wax.

Method of construction

Water is not used in nest excavation. A burrow is initiated at a shallow angle to the ground surface. Soil is extracted using the mandibles, the bee continuously turning on its long axis. The spoils of excavation are raked out of the nest and accumulate to one side of the nest. In densely populated nesting aggregations there are no distinct tumuli, the entire surface of the compacted clayey ground becoming covered with destructured soil. An entrance to a well established nest is concealed with loose earth through which the bee digs when entering.

Associated insects

During the nesting season female *Thyreus* have repeatedly been observed in attendance at and digging through closures of nests of *A. (Z.) punctifrons* on the farms Thursford and Clifton strongly suggesting a parasitic association. A sample of eight was constituted of seven *Thyreus alfeni* (Brauns), three from Thursford and four from Clifton, and one *Thyreus delumbatus* (Vachal) from Clifton. Brauns (1913) recorded that the latter (as *Crocisa braunsiana* Friese) was present in large numbers in association with the nesting aggregations of *A. (Z.) punctifrons* (as *Anthophora circulata*) at Willowmore and, though he gives no further evidence, refers to it as a regular parasite.

It is of interest that *T. delumbatus* was collected in company with its putative host visiting flowers of *B. capensis* on Clifton.

A single female mutillid was observed digging through the loose earth closure of a nest on Thursford suggesting a parasitic association.

***Anthophora (Heliophila) praecox* Friese**

Geographic distribution

Anthophora (Heliophila) praecox Friese has been recorded from the western, southern and eastern Cape Province, from the eastern Orange Free State and Lesotho (Eardley and Brooks 1989, Fig. 108).

Nesting areas, nest sites and density

Two nesting areas of *A. (H.) praecox* have been located, Hilton Farm (27.15S, 32.21E), Grahamstown and Tierberg Farm (33.08S, 22.16E), Prince Albert. Nesting sites in both areas were water cut vertical banks, in the former a river bank and in the latter the bank of an erosion gully. On Tierberg the bee was also found nesting in an artificial vertical bank, the mud wall of a ruined building. Nesting in the walls of buildings was previously noted by Brauns (1913) who observed that *A. (H.) praecox* (as *A. wartmanni* var. *praecox* Friese) in Willowmore was often found nesting in large numbers close together in walls constructed of unbaked bricks. The nests on Hilton and Tierberg were also similarly crowded together.

Flower visiting and provision

Anthophora (H.) praecox has been collected on the yellow flowers of *Berkheya* species (Asteraceae) from the Olifants River Valley in the west to Hilton Farm, Grahamstown in the east. In addition it has been collected on flowers of *Sphalmanthus* sp. (Mesembryanthemaceae) at Klein Doorn River, 10 km E Lemoenshoek, and on the blue flowers of *Anchusa capensis* Thunberg (Boraginaceae) on Hilton Farm. Voucher specimens are listed in Appendix 1.

This bee was not collected on flowers on Tierberg farm but pollen from provision from nest cells was compared microscopically with that of plants growing in the vicinity of the nests and was found to match that of *Pentzia incana* (Asteraceae).

The cells from the Hilton nests had been provisioned with a very wet but not fluid orange pollen and nectar mixture which filled the cells to within 5 mm of the seal. The surface of the provision was smooth.

Description of the nest

The nest, which is sited in a vertical compacted earthen bank, is a single-celled to multi-celled burrow, in some instances with at least two cells in linear series. Access to the burrow is by a simple entrance hole without any form of entrance turret. The cells are smoothed on the inside, lined with a "varnish" like substance, and closed with a mud seal coated on both surfaces with the same substance as is used for lining the cells.

Method of construction of the nest and oviposition

Nest initiation has not been observed. It was not clear whether the burrows were self-excavated or pre-existing. Those at Hilton were in reddish "sandstone" and the cells had been lined with mud clearly introduced into the nest, suggesting that the burrows might have been pre-existing. No such difference between the substrate and the cell lining was observed in the Tierberg burrows. The burrows in the erosion gully were crowded together and apparently interlinked sharing more than one entrance and a single entrance being entered by more than one female, suggesting nest sharing.

A single egg was obtained from a horizontally positioned cell from a Hilton nest. It was white, curved, 3.5 mm long and 0.75 mm wide at mid-length and had been laid onto the vertical surface of the provision. It was only attached by the upper end, the rest of the egg hanging free from the provision.

Associated insects

No direct evidence for nest parasitism was obtained; however, *Thyreus calceatus* (Vachal) was commonly in attendance at the nests in the river bank at Hilton.

Anthophora (Paramegilla) epichariformis Gribodo

Geographic distribution

Anthophora (Paramegilla) epichariformis Gribodo has been recorded from the southwestern Cape (Eardley and Brooks 1989). A nesting female and a male collected on the farm Tierberg (33.08S, 22.16E) to the east of Prince Albert in the southern Great Karoo (26.xi.-5.xii.1987, F.W., S.K. and

R.W.Gess) extends the known distribution eastwards.

Nesting area and nest site

One nest of *A. (P.) epichariformis* was located on the farm Tierberg. It was situated near the base of a high, subvertical, south-facing bank of the Tierberg River and sited beneath an overhang. The river bank is constituted of a grey poorly sorted unconsolidated modern alluvium.

Flower visiting and provision

There appear to be no flower visiting records; however, pollen taken from the provision of the three cells obtained from the excavated nest was all of one kind and matched that of a *Pteronia* species (Asteraceae) growing in the vicinity of the nest.

The provision was a moist pollen and nectar mass.

Description of the nest and egg

The single nest obtained consisted of a burrow excavated in the river bank. There was no entrance turret. The shaft penetrated the bank horizontally for 2 cm and then turned at right angles to run subvertically downwards more-or-less parallel to the surface of the bank to a depth of 10 cm terminating in three cells in linear series each sealed with mud. The walls of the cells were cemented and lined with a waxy coating.

The egg, which is laid onto the surface of the provision, is curved, yellow and 4.5 mm long from tip to tip across the arc.

Method of construction of the nest

Water did not appear to have been used for the excavation of the burrow. The nature of the bonding agent used for cementing the walls of the cell and sealing the cells was not identified.

DISCUSSION OF NESTING BY *AMEGILLA* AND TWO SUBGENERA OF *ANTHOPHORA*,
HELIOPHILA AND *PARAMEGILLA*

The most detailed description of the nesting of an *Amegilla* is that of Houston (1991) for the Australian *Amegilla (Asaropoda) dawsoni* (Rayment). Further nesting accounts for Australian *Amegilla* species are for *Amegilla (Asaropoda)* sp. 2 (Houston 1991), *Amegilla (Asaropoda)* sp. (?*bombiformis*, Cardale 1968b), *Amegilla (Asaropoda)* sp. (Maynard 1992), *Amegilla (Zonamegilla) pulchra* (Smith) (Michener 1960, as *A. salteri* (Rayment); Cardale 1968a as *Amegilla (Amegilla) pulchra* (Smith)). Fragmentary notes on several Australian species are given in Rayment (1935, 1951) and on a Palearctic species in Ferton (1920).

Nesting in aggregations as recorded for *A. (Zabr.) punctifrons* seems to be a common feature of *Amegilla*. Single widely scattered nests as recorded for *A. (M.) atrocincta* is less common. However, the nests of *A. (A.) dawsoni* though they do occur singly and widely scattered are also found in aggregations of up to 10 000. This raises the question of whether there are areas where populations of *A. (M.) atrocincta* are large and whether in such areas this species may also nest in aggregations.

Excavation by *Amegilla* may either be with (for example *A. (M.) atrocincta* and *A. (A.) dawsoni*)

or without the use of a wetting agent (for example *A. (Zebr.) punctifrons*). Whereas water collection by *A. (M.) atrocincta* has been regularly observed, Houston states that no Australian solitary bees are known to visit water. He suggests that nectar may be the wetting agent used in excavation and construction by *A. (A.) dawsoni*. Unfortunately he did not test his hypothesis by analysing the mud used in the construction of the turrets.

Turrets are constructed by some but not all Australian *Amegilla*. The turrets of *A. (M.) atrocincta*, *A. (A.) dawsoni* and Maynard's *A. (A.)* sp. at least, apart from the probable difference in the bonding agent, are initially similarly constructed. However, whereas turrets of up to 80 mm appear to be the norm for *A. (M.) atrocincta*, 15-20 mm is usual for *A. (A.) dawsoni* and 10 mm for Maynard's *A. (A.)* sp.. Associated with the turret of *A. (A.) dawsoni* is a pronounced annular tumulus whereas there were no visible deposits of discarded soil in the vicinity of the nests of *A. (M.) atrocincta*. Deposits of discarded soil are, however, characteristic of *A. (Zebr.) punctifrons* which does not construct a turret but keeps the nest entrance closed with loose material excavated from the shaft.

Multicellular burrows seem to be characteristic for *Amegilla* but the arrangement of secondary shafts and cells differs markedly between species. The single-celled burrows of *A. (M.) atrocincta*, *A. (A.) dawsoni* and Houston's species 2 are similar in that they all terminate in a vertical cell with a double seal above which is a soil filled antechamber. However, burrows with more than one cell are markedly distinct. If the single two-celled nest of *A. (M.) atrocincta* is taken as typical for the species then the secondary shaft in nests of this species diverges from the main shaft immediately within the entrance, extends laterally and then downwards ending in a cell at approximately the same depth as the first cell. However, the main shafts of *A. (A.) dawsoni* and Houston's species 2 remain unbranched until immediately above the antechamber at which point there is a lateral and downward extension leading to a second cell. As each successive cell of *A. (A.) dawsoni* is deeper than that preceeding it the main shaft appears to continue downward in steps. However, succeeding cells of species 2 form a group all at the same depth. Whereas cells in linear series have not been recorded for *A. (M.) atrocincta* and species 2 they seem to be usual for *A. (Zon.) pulchra* and *A. (Zebr.) punctifrons* and occasionally two cells in sequence are constructed by *A. (A.) dawsoni*.

Lining of the cells with wax which is presumed to be derived from the Dufour's gland secretion seems to be general in the Anthophorini. *A. (M.) atrocincta* and *A. (Asaropoda)* species waterproof the cell seal with wax. The way in which this is achieved appears to differ but this may reflect a difference in interpretation. Houston considers the mud seal of *A. (A.) dawsoni* to be constructed spirally and to be waxed on the lower surface just before the central aperture is finally sealed with mud. From the small sample of *A. (M.) atrocincta* seals, all completed, available to the present authors it appears that this species applies the wax together with the mud as the wax on the lower surface extends across the final central application of mud and is also present on the upper surface. Both species construct a second unwaxed seal above the first seal, fill the antechamber with soil and then construct a third seal.

A knowledge of the nesting of more species is required before it will be possible to distinguish between subgeneric and specific differences.

The notes on the nesting of *Anthophora (Heliophila) praecox* and *Anthophora (Paramegilla) epichariformis* presented here though scanty are of interest when considered together with the other published observations for the two subgenera to which they belong.

Nesting in turretless burrows in aggregations in vertical to subvertical earthen banks has, in addition to *Anthophora (H.) praecox*, been recorded for *Anthophora (Heliophila) braunsiana* Friese (Rozen 1969) and *Anthophora (Heliophila) rufolanata* Dours (Rozen 1969 as *Anthophora krebsi* Friese) in the eastern Cape Province, South Africa, and *Anthophora (Heliophila) flexipes* Cresson

(Torchio and Youssef 1968 as *Anthophora* (*Micranthophora*) *flexipes* Cresson) and *Anthophora* (*Heliophila*) *peritomae* Cockerell (Torchio 1971 as *Anthophora* (*Micranthophora*) *peritomae* Cockerell) in Utah, U.S.A. A sixth species of *Anthophora* (*Heliophila*), *Anthophora* (*H.*) *vestita* Smith, has been recorded nesting in vertical earthen surfaces, walls built of unbaked, sundried clay bricks (Brauns 1913). Unfortunately no details of the nests are given.

Entrance sharing as observed for *A. (H.) praecox*, has been recorded by Torchio (1971) for *A. (H.) peritomae* Cockerell, similarly nesting in a bank honeycombed with burrows.

Instances of at least two cells arranged in linear series have been recorded for all but *A. (H.) rufolanata*. As this practice is variable it is possible that instances may be found to occur for this species in addition.

Little seems to have been recorded on the nesting of *Anthophora* (*Paramegilla*). Ferton (1902, 1920) gives notes on the nesting of *A. (Paramegilla) bahueorum* Lepeletier and *A. (Paramegilla) ferruginea* Lepeletier in France. Both, like *A. (P.) epichariformis* excavate turretless, multicellular nests. *A. (P.) ferruginea* unlike the other two species seemingly nests in horizontal ground rather than in vertical banks. As only a single nest of *A. (P.) epichariformis* is known it could not be established whether or not the linear arrangement of the cells is the rule. In Ferton's nests of *A. (P.) ferruginea* only some of the cells were arranged in linear sequence. It would therefore appear that even within single nests of *A. (Paramegilla)* as in *A. (Heliophila)* this is a variable character. Brooks (1988) mentions that Marikovskaya (1970) has described nests of two Eurasian species of *A. (Paramegilla)* but gives no details.

ANALYSIS AND DISCUSSION OF FLOWER VISITING BY SOUTHERN AFRICAN ANTHOPHORINI

The Anthophorini, that is *Amegilla* and *Anthophora*, are regarded as polylectic [collecting pollen from a wide range of families] as a general rule, narrow oligolecty [collection of pollen from flowers of a single family or even genus] being considered unusual (Brooks 1988). Most collectors when recording flowers visited do not distinguish between pollen and nectar collection. The data for southern African Anthophorini available to the authors in the present discussion should therefore be seen as encompassing both types of visit indiscriminately. They are assembled from label data in the Albany Museum collection (F.W., S.K., D.W., H.W. and R.W.Gess - 339 records, and C.F.Jacot Guillaumod - 54 records) and from label data of other collectors (a total of 109 records) listed by Eardley and Brooks (1989) and Eardley (1994). Records are available for 16 of the 31 species of *Amegilla* and 10 of the 31 species of *Anthophora* represented in southern Africa. Twenty four dicot families and three monocot families in total have been recorded as visited. Tables 1 and 2 indicate the families known to be visited by each of the species. Immediately apparent are some interesting differences between *Amegilla* and *Anthophora*, and between the two subgenera (*Heliophila* and *Pyganthophora*) of *Anthophora* for which records are available.

Taking the 16 species of *Amegilla* together, Acanthaceae appears to be markedly favoured being recorded for 12 (75.00%) of the species as compared with one (10.00%) of the ten species of *Anthophora*. By contrast seven (70.00%) of the ten species of *Anthophora* were recorded from Boraginaceae whereas of the 16 species of *Amegilla* only one (6.25%) was recorded from this plant family. Furthermore five (50.00%) of the ten species of *Anthophora* were recorded from Asteraceae and from Sterculiaceae whereas of the 16 species of *Amegilla* only six (37.50%) and two (12.50%) respectively were recorded from these plant families. However, Asteraceae together with the equally ranked Lamiaceae does come second as being most favoured after Acanthaceae by *Amegilla* as a whole.

TABLE 1. Flower families recorded as visited by 16 *Amegilla* spp. together with the number and percentage of these species visiting each flower family (the species here represented by numbers correspond to the species listed by number in Appendix 1).

Flower families	Amegilla species																no.	%
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	of spp.	
Acanthaceae	+	+	+	+	+	+	+	-	-	+	+	-	-	+	+	+	12	75.00
Asteraceae	-	-	+	-	-	+	+	-	-	+	+	-	-	-	-	+	6	37.50
Boraginaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Campanulaceae	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	2	12.50
Capparaceae	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	3	18.75
Convolvulaceae	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	1	6.25
Elatinaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Geraniaceae	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	+	3	18.75
Hydrophyllaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Lamiaceae	-	-	+	+	-	-	+	-	-	-	+	-	+	-	-	+	6	37.50
Malvaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Melastomataceae	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	1	6.25
Mesembryanthemaceae	-	-	-	-	-	-	+	+	-	-	-	-	-	-	+	+	4	25.00
Mimosaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	2	12.50
Moringaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Papilionaceae	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	2	12.50
Pedaliaceae	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	+	3	18.75
Plumbaginaceae	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	+	3	18.75
Proteaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	6.25
Rosaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Scrophulariaceae	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	1	6.25
Selaginaceae	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	2	12.50
Solanaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	6.25
Sterculiaceae	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	2	12.50
Zygophyllaceae	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	3	18.75
Liliaceae	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	2	12.50
no. of flower fams for each bee sp.	1	2	6	2	2	2	15	3	1	2	5	1	4	1	2	14		

The records for the subgenera *Heliophila* and *Pygauthophora* suggest differences in forage flower choice. For example, sampling of flower visitors to Asteraceae has yielded five species of *Heliophila* but no *Pygauthophora*. On the other hand sampling of Zygophyllaceae has yielded four species of *Pygauthophora* but no *Heliophila*. The association with Asteraceae exhibited by these five *Heliophila* species of the Old World Vestita Species Group taken together with the comment of Brooks (1988), reviewing the accounts of Torchio and Youssef (1968) and Torchio (1971), that there is a definite preference by the New World Estebana Species Group for Asteraceae, strengthens an association between the subgenus *Heliophila* and Asteraceae.

GESS AND GESS: NESTING AND FLOWER VISITING OF SOME SOUTHERN AFRICAN ANTHOPHORINI

TABLE 2. Flower families recorded as visited by 10 *Anthophora* spp., 5 each of the subgenera *Heliophila* and *Pyganthophora*, together with the number and percentage of these species visiting each flower family (the species here represented by numbers correspond to the species listed by number in Appendix 1).

Flower families	Anthophora species										no. of spp.			% of spp.
	Heliophila					Pyganthophora					H	P	H+P	
	17	18	19	20	21	22	23	24	25	26				
Acanthaceae	-	-	-	+	-	-	-	-	-	-	1	0	1	10.00
Asteraceae	+	+	+	+	+	-	-	-	-	-	5	0	5	50.00
Boraginaceae	-	+	+	+	+	-	-	+	+	+	4	3	7	70.00
Campanulaceae	-	-	-	-	+	-	-	-	-	-	1	0	1	10.00
Lamiaceae	+	-	-	+	-	-	-	-	-	-	2	0	2	20.00
Mesembryanthemaceae	-	-	-	-	-	+	-	+	+	-	0	3	3	30.00
Sterculiaceae	-	-	-	-	+	+	-	+	+	+	1	4	5	50.00
Solanaceae	-	-	-	-	-	-	+	-	-	-	0	1	1	10.00
Zygophyllaceae	-	-	-	-	-	-	+	+	+	+	0	4	4	40.00
Haemodoraceae	-	-	-	-	+	-	-	-	-	-	1	0	1	10.00
Iridaceae	-	-	-	-	+	-	-	-	-	-	1	0	1	10.00
no. of flower fams for each bee sp.	2	2	2	4	6	2	2	4	4	3				

Clearly there are too few records available to draw any firm conclusions. However, the differences in flower choice between genera and also between subgenera (despite the lack of distinction between pollen and nectar collection) indicate that the southern African Anthophorini do not as a rule practise indiscriminate broad polylecty.

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Appendix 1

Catalogue of flower visiting records for the Anthophorini (all records Albany Museum collection except those marked * which are taken from Eardley and Brooks 1989 and Eardley 1994).

abbreviations - colours: B = blue; BV = bluish violet; G = green; O = orange; Pi = pink; PiV = pinkish violet; Pu = purple; PuV = purplish violet; V = violet; W = white; WY = cream; Y = yellow;
sex: F = female; M = male.
areas: CP = Cape Province; Nam. = Namibia; Nat. = Natal; Tvl = Transvaal; Richtersveld N Park = Richtersveld National Park.

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Anthophorini

Amegilla Friese

1. *Amegilla (Acknonopsis) minadveua* (Cockerell)
 - Acanthaceae
 - Isoglossa* Derst.
 - **I.* sp. - - - ? Durban, Nat.; Cockerell, 1930
2. *Amegilla (Aframegilla) nubica* (Lepeletier)
 - Acanthaceae
 - Moneclma* Hochst.
 - M. mollissimum* (Nees) P.G.Mey. Pi F 1 Richtersveld N Park, CP; FW,SK&RWGess, 24.ix.95
 - Pedaliaceae
 - Sesamum* L.
 - **S.* sp. - M 1 S Leonardoville, Nam.; VBWhitehead, 11.ii.84
3. *Amegilla (Amegilla) capensis* (Friese)
 - Acanthaceae
 - *- - - Wolkberg, Tvl; RHWatmough, -.iv.74
 - Asteraceae (Compositae)
 - Othouua* L.
 - **O.* sp.; Cockerell, 1908
 - Geigeria* Griesselich
 - **G.* sp.; Cockerell, 1908
 - Convolvulaceae
 - Convolvulus* L.
 - **C.* sp. - F 1 Angola; Cockerell, 1907
 - Lamiaceae
 - Plectranthus* L'Herit.
 - **P.* sp. - F 2 Katberg Pass, CP; VBWhitehead, 25.xi.85
 - *- - - Wolkberg, Tvl; RHWatmough, -.iv.74
 - Melastomataceae
 - Dissotis* Benth.
 - **D.* sp. - F 2 Chimanimani Mts, Moz.; RHWatmough, 3.iv.72
 - Selaginaceae
 - Walafrida* E.Mey.
 - **W.* sp. - F 1 N Edenburg, Tvl; MJohannsmeier, -.-.
4. *Amegilla (Amegilla) natalensis* (Friese)
 - Acanthaceae
 - *- - - Wolkberg, Tvl; RHWatmough, -.iv.74
 - Lamiaceae
 - *- - - Wolkberg, Tvl; RHWatmough, -.iv.74
5. *Amegilla (Megamegilla) acraeusis* (Fabricius)
 - Acanthaceae
 - Blepharis* Juss.
 - B. capensis* (L. f.) Pers. W F 1 Grahamstown, CP; DWGess, 3.ii.81
 - B. capensis* (L. f.) Pers. W M 3 Grahamstown, CP; DWGess, 3.ii.81

Plumbaginaceae

**Limonium* Mill.

- M 1 Bredasdorp, CP; CDEardley, 15.xi.82

6. *Amegilla* (*Micramegilla*) *atrocineta* (Lepeletier)

Acanthaceae

Blepharis Juss.*B. capensis* (L.f.) Pers.

W M 1 Grahamstown, CP; FWGess, 5.i.79

B. capensis (L.f.) Pers.

W F 6 Grahamstown, CP; FW&DWGess, 7.i.79

B. capensis (L.f.) Pers.

W M 8 Grahamstown, CP; FW&DWGess, 7.i.79

B. capensis (L.f.) Pers.

W F 2 Grahamstown, CP; FW&DWGess, 15.i.81

B. capensis (L.f.) Pers.

W F 4 Grahamstown, CP; FW&DWGess, 3.ii.81

B. capensis (L.f.) Pers.

W F 5 Grahamstown, CP; FW,DW&RWGess, 8.ii.81

B. capensis (L.f.) Pers.

W F 2 Waterford, CP; RWGess, 25.xi.87

Asteraceae (Compositae)

Berkleya Ehrh.*B. heterophylla* (Th.) O.Hoffm.

Y M 1 Grahamstown, CP; FW&SKGess, 20.xi.90

7. *Amegilla* (*Micramegilla*) *niveata* (Friesie)

Acanthaceae

Blepharis Juss.*B. capensis* (L.f.) Pers.

W F 1 Waterford, CP; RWGess, 25.xi.87

Moneclima Hochst.*M. mollissimum* (Nees) P.G.Mey.Pi F 5 Richtersveld N Park, CP;
FW,SK,&RWGess, 18-24.ix.95*M. mollissimum* (Nees) P.G.Mey.Pi M 1 Richtersveld N Park, CP; FW,SK,&RWGess,
18-24.ix.95**M. sp.*

- F 18 Usakos, Nam.; RHWatmough, 5.vii.75

**M. sp.*

- M 7 Usakos, Nam.; RHWatmough, 5.vii.75

Peristrophe Nees*P. cernua* Nees

V F 1 Grahamstown, CP; FWGess, 3.xii.81

Petalidium Nees**P. sp.*

- F 2 Ou Lutzputz, CP; VBWhitehead, 31.vii.84

"acanth"

W M 2 Richtersveld N Park, CP; FW,SK,&RWGess,
24.ix.95

Aizoaceae: Mesembryanthema (Mesembryanthemaceae)

Mesembryanthemum L.**M. crystallinum* Hook.f.

W F 3 SW Kakamas, CP; VBWhitehead, 6.ii.84

**M. sp.*

- F 1 Jakkalsputs, CP; VBWhitehead, 21.xi.75

**M. sp.*

W F 1 Klinghardtberge, Nam.; RHWatmough, 19.x.74

**M. sp.*

O F 2 Aurusberg, Nam.; RHWatmough, 23.x.74

"mesem"

W F 3 Montagu/Matrosberg, CP; SK&RWGess, 4.xii.86

"mesem"

W F 2 Matrosberg, CP; RWGess, 4.xii.86

Asteraceae (Compositae)

Berkleya Ehrh.*B. carlinifolia* (DC.) Roessler

Y M 1 ENE Ceres, CP; HWGess, 29-30.xi.89

**B. rigida* (Thunb.) H.Bol. &Wolley-Dod ex Adamson &
SalterY F 2 SE Hopefield, CP; JGRozen *et al.*, 15.x.72

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<i>Senecio</i> L.				
	<i>S. rosmarinifolius</i> L. f.	Y	F	2 Oudtshoorn, CP; FW&RWGess, 7-8.xii.86
Boraginaceae				
<i>Anchusa</i> L.				
	<i>A. capensis</i> Thunb.	B	F	1 Kamieskroon, CP; FW&SKGess, 9.x.94
	<i>A. capensis</i> Thunb.	B	F	1 Kamieskroon, CP; FW,SK&RWGess, 28.ix.95
<i>Lobostemon</i> Lehm.				
	<i>L. sp.</i>	B	F	4 Clanwilliam/Graafwater, CP; FW&SKGess, 4.x.90
Capparaceae				
<i>Cleome</i> L.				
	<i>C. paxii</i> (Schinz) Gilg & Ben.	Y	F	1 Richtersveld N Park, CP; FW,SK&RWGess, 16.ix.95
<i>Maerua</i> Forssk.				
	<i>M. schinzii</i> Pax	W	M	1 Vioolsdrif, CP; FW&SKGess, 3.x.85
Elatinaceae				
<i>Bergia</i> L.				
	<i>B. glomerata</i> L.f.	G	F	1 Grahamstown, CP; FW&SKGess, 20.xi.90
Geraniaceae				
<i>Geranium</i> L.				
	* <i>G. sp.</i>	-	F	1 Aussenkehr, Nam.; VBWhitehead, 16.ix.83
	* <i>G. sp.</i>	-	M	1 Aussenkehr, Nam.; VBWhitehead, 16.ix.83
Hydrophyllaceae				
<i>Codon</i> L.				
	<i>C. royerii</i> L.	W	F	1 Richtersveld N Park, CP; FW,SK&RWGess, 19.ix.95
Lamiaceae (Labiatae)				
	"labiate"	V	F	2 Ouberg Pass, Montagu, CP; FWGess, 3.xii.86
	"labiate"	B	F	1 Nieuwoudtville, CP; FW&SKGess, 3-8.x.89
	*"labiate"	B	F	1 Aurusberg, Nam.; RHWatmough, 23.x.74
Malvaceae				
	*_	-	F	1 Klinghardtberge, Nam.; RHWatmough, 19.x.74
Mimosaceae				
<i>Acacia</i> Mill.				
	<i>A. caffra</i> (Thunb.) Willd.	WY	M	1 Oudtshoorn, CP; RWGess, 9-12.xii.86
Moringaceae				
<i>Moringa</i> Adans.				
	* <i>M. ovalifolia</i> Dinter & Berger	-	F	1 Gobabeb, Nam.; MLPenrith&SLouw, 18.ii.-20.iii.83
Pedaliaceae				
<i>Harpagophytum</i> DC. ex Meissn.				
	* <i>H. procumbens</i> (Burch.) DC. ex Meissn.	-	F	1 E Kimberley, CP; VBWhitehead, 19.i.84
<i>Sesamum</i> L.				
	* <i>S. triphyllum</i> Welw. ex Aschers.	-	F	1 Derm, Nam.; VBWhitehead, 10.ii.84

- **S. sp.* - F 1 W Boshoff, CP; VBWhitehead, 19.i.84
 **S. sp.* - F 1 Harmonie, CP; VBWhitehead, 25.ii.80
- Rosaceae
Neuradopsis Brem. & Oberm.
 **N. sp.* - F 2 Leonardville, Nam.; VBWhitehead, 15.iv.81
- Scrophulariaceae
Aptosimum Burch.
A. indivisum Burch. ex Benth. BV F 1 Springbok, CP; FW&SKGess, 8.x.94
A. spinescens (Thunb.) Weber PuV F 1 Springbok, CP; SKGess, 15-21.x.87
Peliostomum Benth.
P. leucorrhizum E.Mey. V F 1 Richtersveld N Park, CP; FW,SK&RWGess, 19.ix.95
 ex Benth.
- Sterculiaceae
Hermannia L.
H. disermifolia Jacq. Y F 1 Nieuwoudtville, CP; FW&SKGess, 29.ix.94
H. disermifolia Jacq. Y F 1 Kamieskroon, CP; FW&SKGess, 10.x.94
- Zygophyllaceae
Tribulus L.
 **T. sp.* Y F 1 N Kakamas, CP; VBWhitehead, 7.ii.84
 **T. sp.* Y M 1 N Kakamas, CP; VBWhitehead, 7.ii.84
 **T. sp.* Y M 1 W Mariental, Nam.; RG Oberprieler, 22.iii.83
Zygophyllum L.
Z. sp. Y F 1 Nieuwoudtville, CP; FW&SKGess, 2.x.89
8. *Amegilla (Micramegilla) velutina* (Friese)
 Aizoaceae: Mesembryanthema (Mesembryanthemaceae)
Psilocanlon N.E.Br.
 **P. sp.* - F 1 Noordoewer, Nam.; VBWhitehead, 7.iii.80
 **P. sp.* - M 3 Noordoewer, Nam.; VBWhitehead, 7.iii.80
 ?*Stoebria* sp. W F 4 Richtersveld N Park, CP; FW,SK&RWGess, 16.ix.95
- Capparaceae
Cleome L.
C. paxii (Schinz) Gilg & Ben. Y F 13 Richtersveld N Park, CP; FW,SK&RWGess, 16.ix.95
- Geraniaceae
Geranium L.
 **G. sp.* - F 1 Aussenkehr, Nam.; VBWhitehead, 16.ix.83
 **G. sp.* - M 2 Aussenkehr, Nam.; VBWhitehead, 16.ix.83
9. *Amegilla (Zebramegilla) bechuanensis* (Cockerell)
 Capparaceae
Cleome L.
 **C. angustifolia* Forssk. - F 1 nr Vivo, Tvl; CDEardley, 3.ii.84
10. *Amegilla (Zebramegilla) calens* (Lepelletier)
 Acanthaceae
Blepharis Juss.
B. capensis (L.f.) Pers. W F 1 Grahamstown, CP; FWGess, 7.i.79

- | | | |
|---|---------|---|
| <i>B. capensis</i> (L.f.) Pers. | W F 8 | Grahamstown, CP; FW&DWGess, 7.i.79 |
| <i>B. capensis</i> (L.f.) Pers. | W M 1 | Grahamstown, CP; FW&DWGess, 7.i.79 |
| <i>B. capensis</i> (L.f.) Pers. | W F 1 | Grahamstown, CP; FWGess, 8.ii.81 |
| <i>B. capensis</i> (L.f.) Pers. | W F 2 | Grahamstown, CP; FWGess, 10.ii.86 |
| 15. <i>Amegilla</i> (<i>Zebramegilla</i>) <i>punctifrons</i> (Walker) | | |
| Acanthaceae | | |
| <i>Blepharis</i> Juss. | | |
| <i>B. capensis</i> (L.f.) Pers. | W M 2 | Grahamstown, CP; FW&SKGess, 27.x.72 |
| <i>B. capensis</i> (L.f.) Pers. | W F 1 | Grahamstown, CP; DWGess, 5.i.79 |
| <i>B. capensis</i> (L.f.) Pers. | W F 1 | Grahamstown, CP; FW&DWGess, 7.i.79 |
| <i>B. capensis</i> (L.f.) Pers. | W M 7 | Grahamstown, CP; FW&DWGess, 7.i.79 |
| <i>B. capensis</i> (L.f.) Pers. | W F 6 | Grahamstown, CP; DW&RWGess, 15.i.81 |
| <i>B. capensis</i> (L.f.) Pers. | W F 5 | Grahamstown, CP; DWGess, 3.ii.81 |
| <i>B. capensis</i> (L.f.) Pers. | W F 3 | Grahamstown, CP; FW&SKGess, 8.ii.81 |
| Aizoaceae: Mesembryanthema (Mesembryanthemaceae) | | |
| "mesem" | WY M 1 | Kommadagga, CP; FW&SKGess, 23.x.85 |
| 16. <i>Amegilla</i> (<i>Zebramegilla</i>) <i>spilostoma</i> (Cameron) | | |
| Acanthaceae | | |
| <i>Blepharis</i> Juss. | | |
| <i>B. capensis</i> (L.f.) Pers. | W M 2 | Grahamstown, CP; FW&SKGess, 27.x.72 |
| Aizoaceae: Mesembryanthema (Mesembryanthemaceae) | | |
| <i>Mesembryanthemum</i> L. | | |
| * <i>M. crystallinum</i> Hook.f. | W F 1 | Onrusrivier, CP; VBWhitehead, 17.i.76 |
| <i>Psilocaulon</i> N.E.Br. | | |
| <i>P. acutisepalum</i> (Berger) | WPi F 2 | Heerenlogement, CP; FW,SK&RWGess, 8.x.95 |
| N.E.Br. | | |
| <i>P. cf. subnodosum</i> (Berger) | Pi F 1 | Graafwater, CP; FW,SK&RWGess, 6.x.95 |
| N.E.Br. | | |
| "mesem" | W F 1 | Montagu/Matroosberg, CP; FWGess, 4.xii.86 |
| Asteraceae (Compositae) | | |
| <i>Senecio</i> L. | | |
| <i>S. linifolius</i> L. | Y F 2 | Grahamstown, CP; CFJacotGuillarmod, 27.i.75 |
| <i>S. linifolius</i> L. | Y M 2 | Grahamstown, CP; CFJacotGuillarmod, 27.i.75 |
| <i>S. linifolius</i> L. | Y M 3 | Grahamstown, CP; CFJacotGuillarmod, 31.i.75 |
| <i>S. linifolius</i> L. | Y F 1 | Grahamstown, CP; CFJacotGuillarmod, 2.ii.75 |
| <i>S. linifolius</i> L. | Y M 3 | Grahamstown, CP; CFJacotGuillarmod, 2.ii.75 |
| Campanulaceae | | |
| <i>Cyphia</i> Berg. | | |
| <i>C. sp.</i> | PiV M 1 | Grahamstown, CP; FWGess, 21.iii.78 |
| Geraniaceae | | |
| <i>Pelargonium</i> L' Herit | | |
| <i>P. myrrhifolium</i> Ait. | - F 1 | Oudtshoorn, CP; CFJacotGuillarmod, 10.x.72 |
| <i>P. myrrhifolium</i> Ait. | - M 1 | Oudtshoorn, CP; CFJacotGuillarmod, 10.x.72 |
| Lamiaceae (Labiatae) | | |
| <i>Acrotome</i> Benth. | | |
| <i>A. inflata</i> Benth. | BV M 5 | Grahamstown, CP; SKGess, 17.iii.78 |
| <i>A. inflata</i> Benth. | BV M 1 | Grahamstown, CP; FWGess, 21.iii.78 |

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<i>Salvia dentata</i> Ait.	B	F	2	Clanwilliam, CP; FW&SKGess, 4.x.90
* <i>S. sp.</i>	-	M	1	Queenstown, CP; VBWhitehead, 29.xii.83
Liliaceae				
<i>Aloe sp.</i>	Y	F	1	Grahamstown, CP; FWGess, 6.i.81
Mimosaceae				
<i>Acacia</i> Mill.				
<i>A. caffra</i> (Thunb.) Willd.	WY	F	1	Oudtshoorn, CP; RWGess, 9-12.xii.86
<i>A. karroo</i> Hayne	Y	F	1	Colesberg, CP; DWGess, 19.i.85
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. chortophila</i> Ecklon & Zeyher	Y	F	1	Riebeek East, CP; FW&SKGess, 14.xi.92
<i>Psoralea</i> L.				
<i>P. pinnata</i> L.	B	M	2	Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
<i>P. pinnata</i> L.	B	F	2	Grahamstown, CP; CFJacotGuillarmod, 9.ii.75
<i>P. pinnata</i> L.	B	M	3	Grahamstown, CP; CFJacotGuillarmod, 9.ii.75
Pedaliaceae				
<i>Sesamum</i> L.				
* <i>S. sp.</i>	-	F	1	W Boshoff, CP; VBWhitehead, 19.iii.84
Plumbaginaceae				
<i>Limonium</i> Mill.				
* <i>L. sp.</i>	-	F	1	Bredasdorp, CP; CDEardley, 15.xi.82
Proteaceae				
<i>Paranomus</i> Salisb.				
<i>P. bracteolaris</i> Salisb. ex Knight	Pi	F	1	Nieuwoudtville, CP; FW&SKGess, 30.ix.90
Solanaceae				
<i>Lycium</i> L.				
<i>L. sp.</i>	V	M	1	Grahamstown, CP; FW&SKGess, 29.ix.77
* <i>-</i>	-	F	1	Queenstown, CP; VBWhitehead, -.i.64
Zygophyllaceae				
<i>Zygophyllum</i> L.				
<i>Z. sp.</i>	Y	M	3	Nieuwoudtville, CP; FW&SKGess, 28.ix.90

Anthophora Latreille

17. *Anthophora (Heliophila) labrosa* Friese

Asteraceae (Compositae)

<i>Berkheya</i> Ehrh.				
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	2	Grahamstown, CP; FWGess, 12.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	1	Grahamstown, CP; FW&DWGess, 16.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Grahamstown, CP; FW&DWGess, 16.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	1	Grahamstown, CP; FWGess, 25.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	2	Grahamstown, CP; FW&SKGess, 15.xi.77
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	2	Riebeek East, CP; FW&SKGess, 22.xi.82
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Riebeek East, CP; FW&SKGess, 22.xi.82
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Riebeek East, CP; FW&SKGess, 16.x.83
<i>B. sp.</i>	Y	F	1	Clanwilliam, CP; FW&SKGess, 9.x.90

- Senecio* L.
S. linifolius L. Y F 1 Grahamstown, CP; CFJacotGuillarmod, 25.i.75
S. linifolius L. Y F 1 Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
- Lamiaceae (Labiatae)
 "labiate" V M 5 Ouberg Pass, Montagu, CP; FWGess, 3.xii.86
18. *Anthophora (Heliophila) praecox* Friese
 Asteraceae (Compositae)
Berkheya Ehrh.
B. carlinifolia (DC.) Roessler Y M 1 Theronsberg Pass, Ceres, CP; FWGess, 29-30.xi.89
B. heterophylla (Th.) O.Hoffm. Y F 1 Grahamstown, CP; FW&SKGess, 15.xi.77
B. heterophylla (Th.) O.Hoffm. Y F 4 Riebeek East, CP; FW&SKGess, 22.xi.82
B. heterophylla (Th.) O.Hoffm. Y M 1 Riebeek East, CP; FW&SKGess, 16.x.83
B. sp. Y F 1 Clanwilliam, CP; FW&SKGess, 9.x.90
Pentzia Thunb.
P. incana (Thunb.) Kuntze Y F p Prince Albert, CP; SKGess, 26.xi.-5.xii.87
- Boraginaceae
Anchusa L.
A. capensis Thunb. B F 1 Grahamstown, CP; FWGess, 18.xi.77
A. capensis Thunb. B M 2 Grahamstown, CP; FWGess, 18.xi.77
A. capensis Thunb. B M 1 Kamieskroon, CP; FW&SKGess, 11.x.94
19. *Anthophora (Heliophila) rufolanata* Dours
 Asteraceae (Compositae)
Berkheya Ehrh.
B. heterophylla (Th.) O.Hoffm. Y F 2 Grahamstown, CP; FWGess, 12.x.72
B. heterophylla (Th.) O.Hoffm. Y M 4 Grahamstown, CP; FWGess, 12.x.72
B. heterophylla (Th.) O.Hoffm. Y F 5 Grahamstown, CP; FW&DWGess, 16.x.72
B. heterophylla (Th.) O.Hoffm. Y M 1 Grahamstown, CP; FWGess, 16.x.72
B. heterophylla (Th.) O.Hoffm. Y M 3 Grahamstown, CP; FWGess, 25.x.72
B. heterophylla (Th.) O.Hoffm. Y F 1 Riebeek East, CP; FW&SKGess, 16.x.83
Pteronia L.
P. incana (Burm.) DC Y F 2 Kamieskroon, CP; FW&SKGess, 17.ix.92
P. incana (Burm.) DC Y M 1 Kamieskroon, CP; FW&SKGess, 17.ix.92
- Senecio* L.
S. linifolius L. Y F 10 Grahamstown, CP; CFJacotGuillarmod, 25.i.75
S. linifolius L. Y F 1 Grahamstown, CP; CFJacotGuillarmod, 27.i.75
S. linifolius L. Y M 1 Grahamstown, CP; CFJacotGuillarmod, 27.i.75
S. linifolius L. Y F 2 Grahamstown, CP; CFJacotGuillarmod, 31.i.75
S. linifolius L. Y F 4 Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
- Boraginaceae
Anchusa L.
A. capensis Thunb. B M 1 Grahamstown, CP; FWGess, 18.xi.77
A. capensis Thunb. B M 1 Leliefontein, CP; FW,SK&RWGess, 2.x.95
20. *Anthophora (Heliophila) vestita* Smith
 Acanthaceae
Peristrophe Nees
P. cernua Nees V F 1 Grahamstown, CP; FWGess, 3.xii.81
 "acanth" Pi F 6 Morgan Bay, CP; FW&SKGess, 30.iii.-4.iv.89

Asteraceae (Compositae)

Berkheya Ehrh.

<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	8	Grahamstown, CP; FWGess, 12.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Grahamstown, CP; FWGess, 12.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	3	Grahamstown, CP; FW&DWGess, 16.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	5	Grahamstown, CP; FWGess, 25.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	1	Grahamstown, CP; FW&SKGess, 15.xi.77
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Grahamstown, CP; FW&SKGess, 15.xi.77
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	1	Riebeck East, CP; FW,SK&DWGess, 22.xi.82
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Riebeck East, CP; FW,SK&DWGess, 22.xi.82
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	F	2	Grahamstown, CP; FW&SKGess, 20.ix.90
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	3	Grahamstown, CP; FW&SKGess, 20.ix.90

Cirsium Mill. emend. Scop.

<i>C. vulgare</i> (Savi) Ten.	Pu	F	1	Grahamstown, CP; SKGess, 9.iii.78
<i>C. vulgare</i> (Savi) Ten.	Pu	M	2	Grahamstown, CP; SKGess, 9.iii.78

Senecio L.

<i>S. linifolius</i> L.	Y	F	3	Grahamstown, CP; CFJacotGuillarmod, 25.i.75
<i>S. linifolius</i> L.	Y	M	1	Grahamstown, CP; CFJacotGuillarmod, 25.i.75
<i>S. linifolius</i> L.	Y	F	1	Grahamstown, CP; CFJacotGuillarmod, 27.i.75
<i>S. linifolius</i> L.	Y	F	2	Grahamstown, CP; CFJacotGuillarmod, 31.i.75
<i>S. linifolius</i> L.	Y	M	1	Grahamstown, CP; CFJacotGuillarmod, 31.i.75
<i>S. linifolius</i> L.	Y	F	2	Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
<i>S. linifolius</i> L.	Y	M	1	Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
<i>S. sp.</i>	Y	F	1	Grahamstown, CP; FWGess, 28.xii.86

Boraginaceae

Anchusa L.

<i>A. capensis</i> Thunb.	B	F	3	Grahamstown, CP; FWGess, 18.xi.77
<i>A. capensis</i> Thunb.	B	M	7	Grahamstown, CP; FWGess, 18.xi.77

Lamiaceae (Labiatae)

Acrotome Benth.

<i>A. inflata</i> Benth.	BV	M	1	Grahamstown, CP; FWGess, 3.iii.78
<i>A. inflata</i> Benth.	BV	M	2	Grahamstown, CP; SKGess, 17.iii.78

21. *Anthophora (Heliophila) wartmanni* Friese

Asteraceae (Compositae)

Arctotis L.

<i>A. laevis</i> Thunb.	Y	F	1	Clanwilliam, CP; FW&SKGess, 5.x.90
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Berkheya Ehrh.

<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	1	Grahamstown, CP; FWGess, 12.x.72
<i>B. heterophylla</i> (Th.) O.Hoffm.	Y	M	2	Grahamstown, CP; FWGess, 16.x.72

Metalsia R. Br.

<i>M. muricata</i> (L.) D.Don	Pi	F	1	Nieuwoudtville, CP; FW&SKGess, 29.ix.90
<i>M. muricata</i> (L.) D.Don	Pi	F	1	Nieuwoudtville, CP; FW&SKGess, 25.ix.94

Pteronia L.

<i>P. sp. B</i>	Y	F	1	Nababeep, CP; FWGess, 12-13.x.89
<i>P. sp. B</i>	Y	M	1	Nababeep, CP; FWGess, 12-13.x.89

Senecio L.

- S. linifolius* L. Y M 1 Grahamstown, CP; CFJacotGuillarmod, 25.i.75
S. linifolius L. Y F 1 Grahamstown, CP; CFJacotGuillarmod, 31.i.75
S. linifolius L. Y F 1 Grahamstown, CP; CFJacotGuillarmod, 2.ii.75
- Boraginaceae
- Anclusa* L.
A. capensis Thunb. B M 1 Kamieskroon, CP; FW,SK&RWGess, 28.ix.95
A. capensis Thunb. B M 1 Leliefontein, CP; FW,SK&RWGess, 2.x.95
- Campanulaceae
- Wahlenbergia* Schrad. ex Roth
W. sp. V F 1 Nieuwoudtville, CP; FW&SKGess, 30.ix.90
- Haemodioraceae
- Wachendorfia* Burm.
W. sp. Y F 2 Nieuwoudtville, CP; FW&SKGess, 29.ix.90
- Iridaceae
- Homeria* Vent.
H. sp. Y F 1 Nieuwoudtville, CP; FW&SKGess, 28.ix.90
- Scrophulariaceae
- Oftia* Adans.
O. africana (L.) Bocq. W F 1 Graafwater, CP; FW&SKGess, 21.ix.92
22. *Anthophora* (*Pyganthophora*) *abrochia* Eardley & Brooks
- Aizoaceae: Mesembryanthema (Mesembryanthemaceae)
- Herrea* Schwant.
H. sp. Y F 2 Leliefontein, CP; FW&SKGess, 13.ix.92
H. sp. Y F 1 Springbok, CP; FW&SKGess, 8.x.94
H. sp. Y F 3 Springbok, CP; FW,SK&RWGess, 27.ix.95
- Sterculiaceae
- Hernannia* L.
H. disermifolia Jacq. Y F 2 Springbok, CP; FW&SKGess, 8-10.ix.92
H. disermifolia Jacq. Y F 1 Springbok, CP; FW&SKGess, 3.x.94
H. disermifolia Jacq. Y F 3 Kamieskroon, CP; FW&SKGess, 10-11.x.94
H. disermifolia Jacq. Y F 2 Kamieskroon, CP; FW,SK&RWGess, 28.ix.95
H. disermifolia Jacq. Y F 3 Kamieskroon, CP; FW,SK&RWGess, 3.x.95
23. *Anthophora* (*Pyganthophora*) *braunsiana* Fries
- Solanaceae
- Lycium* L.
L. sp. V M 2 Grahamstown, CP; FWGess, 9.iii.78
- Zygophyllaceae
- Zygophyllum* L.
Z. divaricatum Ecklon & Zeyher Y F 1 Leliefontein, CP; FW&SKGess, 13.ix.92
24. *Anthophora* (*Pyganthophora*) *diversipes* Fries
- Aizoaceae: Mesembryanthema (Mesembryanthemaceae)
- Herrea* Schwant.
H. sp. Y F 4 Leliefontein, CP; FW&SKGess, 13.ix.92
- Boraginaceae
- Anchusa* L.
A. capensis Thunb. B M 1 Leliefontein, CP; FW,SK&RWGess, 2.x.95
Lobostemon Lehm.

GESS AND GESS: NESTING AND FLOWER VISITING OF SOME SOUTHERN AFRICAN ANTHOPHORINI

	<i>L. trichotomus</i> DC.	B	F	1	E Pakhuis Pass, CP; DWGess, 3.x.91
	<i>L. trichotomus</i> DC.	B	M	2	E Pakhuis Pass, CP; DWGess, 3.x.91
	<i>L. sp.</i>	B	F	1	Clanwilliam, CP; FW&SKGess, 3.x.90
	Sterculiaceae				
	<i>Hermannia</i> L.				
	<i>H. disermifolia</i> Jacq.	Y	F	1	Kamieskroon, CP; FW&SKGess, 11.x.94
	<i>H. disermifolia</i> Jacq.	Y	F	1	Kamieskroon, CP; FW,SK&RWGess, 28.ix.95
	<i>H. disermifolia</i> Jacq.	Y	F	1	Kamieskroon, CP; FW,SK&RWGess, 3.x.95
	<i>H. sp.</i>	Y	F	2	Graafwater, CP; FW,SK&RWGess, 8.x.95
	Zygophyllaceae				
	<i>Zygophyllum</i> L.				
	<i>Z. divaricatum</i> Ecklon & Zeyher	Y	F	1	Leliefontein, CP; FW&SKGess, 13.ix.92
25. <i>Anthophora</i> (<i>Pyganthophora</i>) <i>krugeri</i> Eardley & Brooks	Aizoaceae: Mesembryanthema (Mesembryanthemaceae)				
	<i>Herrea</i> Schwant.				
	<i>H. sp.</i>	Y	F	2	Leliefontein, CP; FW&SKGess, 13.ix.92
	<i>H. sp.</i>	Y	F	4	Springbok, CP; FW&SKGess, 4-8.x.94
	<i>H. sp.</i>	Y	F	4	Springbok, CP; FW,SK&RWGess, 27.ix.95
	Boraginaceae				
	<i>Anchusa</i> L.				
	<i>A. capensis</i> Thunb.	B	F	3	Leliefontein, CP; FW,SK&RWGess, 2.x.95
	Sterculiaceae				
	<i>Hermannia</i> L.				
	<i>H. disermifolia</i> Jacq.	Y	F	4	Springbok, CP; FW&SKGess, 4-8.x.94
	<i>H. disermifolia</i> Jacq.	Y	F	2	Springbok, CP; FW,SK&RWGess, 27.ix.95
	<i>H. vestita</i> Thunb.	Y	F	1	Ladismith, CP; FW&SKGess, 21.viii.95
	<i>H. sp.</i>	Y	F	1	Graafwater, CP; FW,SK&RWGess, 7.x.95
	Zygophyllaceae				
	<i>Zygophyllum</i> L.				
	<i>Z. divaricatum</i> Ecklon & Zeyher	Y	F	1	Leliefontein, CP; FW&SKGess, 13.ix.92
26. <i>Anthophora</i> (<i>Pyganthophora</i>) <i>schultzei</i> Friese	Boraginaceae				
	<i>?Lobostemon</i> Lehm.				
	<i>?L. sp.</i>	WV	F	1	Nieuwoudtville, CP; FW&SKGess, 25.ix.94
	Sterculiaceae				
	<i>Hermannia</i> L.				
	<i>H. cf. cuneifolia</i> Jacq.	Y	F	1	Nieuwoudtville, CP; FW&SKGess, 30.ix.94
	<i>H. disermifolia</i> Jacq.	Y	F	1	Nieuwoudtville, CP; FW&SKGess, 25.ix.94
	Zygophyllaceae				
	<i>Zygophyllum</i> L.				
	<i>Z. cf. morgsana</i> L.	Y	F	1	Nieuwoudtville, CP; FW&SKGess, 24.ix.94
	<i>Z. cf. morgsana</i> L.	Y	F	1	Nieuwoudtville, CP; FW&SKGess, 26.ix.94
<hr/>					
<i>Anthophora</i> (<i>Paramegilla</i>) <i>leonis</i> Cockerell	Boraginaceae				
	<i>Anchusa</i> L.				
	<i>A. capensis</i> Thunb.	B	M	1	Kamieskroon, CP; FW&SKG, 10.x.94

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**Two small Orthoclaadiinae (Chironomidae, Diptera)
from the Western Cape Province, South Africa**

A.D. HARRISON

Published jointly by the Cape Provincial Museums
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Two Small Orthocladinae (Chironomidae, Diptera) from the Western Cape Province, South Africa

by

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Rondebosch, 7700 South Africa.)

ABSTRACT

All life stages of two small Orthocladinae from mountain streams and rivers in the Western Cape Province are described. *Notocladius capicola*, new genus and species, is very abundant and is able to feed on very small particles scraped off the substratum and must play an important part in the food chain; *Parakiefferiella biloba* Freeman, here described in detail for the first time, is far less abundant and its gut is packed with diatom frustules.

INTRODUCTION

The Chironomidae form an important part of freshwater communities, with many of their larvae feeding on algae and making available the energy from primary production to larger invertebrates and vertebrates. Workers in the field of freshwater research also find chironomid communities useful as indicators of ecological changes taking place in the environment; this makes their correct identification, specially of their larvae and pupae very important. This paper deals with all life stages of two small members of the sub-family Orthocladinae, one is very common in mountain streams and rivers and its larva feeds on very small particles scraped from the rocks. Nevertheless, the adult has not been seen before and shows such peculiar features that a new genus and species has had to be created for it.

METHODS

Adults were caught by sweeping vegetation near streams and rivers; larvae and pupae were caught in nets with fine mesh (< 0.5 mm). All specimens were preserved in 70% or 80% alcohol and mounted in Canada Balsam dissolved in cellosolve. Measurements were made with an eyepiece micrometer and all drawings with a drawing tube on the microscope.

Sources of generic definitions for *Parakiefferiella* are given in the text. Morphological terminology is from Sæther (1980).

Abbreviations used in this paper are:

AR = antennal ratio. Ratio of length of apical flagellomere to combined length of basal flagellomeres.

LR = leg ratio. Ratio of length of tarsomere 1 to length of tibia.

SV = 'Schenkel-Schiene-Verhältnis'. Ratio of femur plus tibiae to tarsomere 1.

BV = 'Beinverhältnisse'. Combined length of femur, tibia and tarsomere 1 divided by length of tarsomeres 2 to 5.

DESCRIPTIONS

Notocladius Gen, nov.*Definition*

ADULT MALE. Small midge with wing length of about 1.00 mm. Head: antenna with 10 flagellomeres, groove beginning at antennomere 3, apex without large subapical seta. No frontal tubercles. Eye hairy, without dorsomesal extension; one outer vertical seta. Tentorium widest at basal half; clypeus normal, palp segment 3 with at least one subterminal sensillum. Thorax: anteprenotal lobes separated by a shallow notch, no scutal tubercle; acrostichals absent; dorsocentrals erect, uniserial; 3 prealars; 2 scutellars. Wing: membrane without setae, very transparent, punctuation very fine; no anal lobe; R_1 and R_{2+3} , later joined by R_{4+5} , fusing with costa to form clavus which terminates before half the wing length; costa not extended; weak false vein from RM to wing tip; Cu straight; wing veins without setae except costa; squama bare. Legs: spurs and comb normal, no pseudospurs; no sensilla chaetica on tarsomere 1 of mid and hind leg; tarsomere 4 short and slightly cordiform; no pulvillae. Hypopygium: no anal point, virga absent; no superior or inferior volsellae; gonostylus simple without crista dorsalis.

ADULT FEMALE. Wing length about 1.1 mm. Head: antenna with 5 flagellomeres, apex without large subapical seta. Eye similar to male, 1 outer vertical seta, no frontal tubercles. Palp similar to male except that segments 2 and 3 are fused. Thorax similar to male. Wings similar to male but clavus comparably longer extending more than halfway to wing tip. Legs similar to male but sensilla chaetica present on tarsomere 1 of mid and hind leg. Genitalia: gonopophysis VIII simple, not divided into ventro-lateral and dorso-medial lobes; gonocoxapodeme of VIII and coxosternapodeme of IX prominent; gonocoxite IX closely applied to body with one seta; postgenital plate of X triangular. Seminal capsules with short necks, ducts convoluted with common opening. Cerci small.

PUPA. Small (1.4 - 1.6 mm). Cephalothorax: setae - frontal setae absent, 2 anteprenotals, 3 small precorneals, 2 widely spaced dorsocentrals. No thoracic horn. Abdomen: posterior single row of small hooks on tergites III - V and on sternites V - VII. Shagreen of small posteriorly pointing spines, none on tergite I, sparse on tergites II - IV, denser on V - VIII forming broad anterior bands; segmental setae small, anal lobe with 3 short macrosetae and no fringe, small lateral denticles present.

LARVA. Small, up to 1.5 mm. long. Antenna: 4 segmented, blade extending to apex of segment 2, Lauterborn organs small, style small. Labrum: seta SI bifid, remaining setae simple; no labial lamella; pecten epipharyngis of 3 subequal scales; some chaetae lateralis enlarged and filmy with ciliary fringe; premandible with 2 teeth, one thin and pointed, the other broad and blunt; no brush. Mandible: apical tooth with 4 inner teeth, seta subdentalis small, seta interna small but with many branches. Mentum: 1 median and 6 pairs of lateral teeth, ventromental plate distinct but small, no beard. Maxilla: palpiger normal, chaetae small, no pecten galearis, lacinal chaetae large, antaxial seta present. Body: parapods normal; procercus about as high as wide with strong setae.

Notocladius capicola spec. nov.

This species is based on a large number of males and females, numerous pupae, some with pharate males, and numerous larvae caught with the pupae and assumed to belong to this species.

ADULT MALE (N=5 mounted and many unmounted)

As per generic definition.

Body length. up to 1.2 mm.

Wing length. 1.0 mm.

Colour. Head and antennae brown; thorax: background creamy yellow, scutal stripes separate and dark brown, setal pits large and light, preepisternum dark brown, legs brown, wings very transparent and colourless; abdomen: tergites I-V dark brown, VI and VII with a narrow brown anterior stripe and the rest yellowish, VIII and hypopygium brown.

Head (Fig. 1). AR 0.25, 10 flagellomeres, apical flagellomere somewhat swollen (Fig. 2), terminal setae small and colourless, mostly sensilla chaetica; eyes hairy; clypeus not swollen; palp segments 16, 12, 28, 62, 102, μm ; 1 subapical sensilla on segment 3.

Thorax. Setation: anteprenotals 0-1, dorsocentrals 9-11, prealars 3, 1 scutellar per side.

Wings (Fig 3). Anal lobe absent, squama bare, length of clavus/winglength (including brachiolum) 0.3. A false vein from clavus almost to wing tip and a second between this and M_{1+2} . Setation: brachiolum 1, no setae on R or M veins.

Legs. Tarsomere 4 short and slightly cordiform (Fig 4). LR fore 0.85, mid 0.63, hind 0.68; SV fore 2.5, BV fore 4.0. No sensilla chaetica on tarsomeres.

Hypopygium (Figs 5, 6 and 7). Anal point absent but 6 anal setae present (Fig. 5). Inferior volsella absent but with row of strong setae in the position where it normally appears in other Orthocladinae (Fig. 6). Gonostylus comparatively small but with large megaseta. Fig. 7 shows the apodemes.

ADULT FEMALE (N=6 mounted, many unmounted)

As per generic definition.

Body length. 1.0 mm.

Wing length. 1.1 mm.

Colour. Similar to male but abdominal tergites uniformly brown.

Head. AR 0.4, 5 flagellomeres. Head setae: 1 outer vertical per side. Palps: segments 2 and 3 are fused but can still be distinguished, 3 has a small terminal projection, lengths 28, 25, 59, 53, 93 μm . 1 subapical sensilla on 3.

Thorax. No scutal tubercle. Setation: lateral anteprenotals nil, dorsocentrals 10, posterior prealars 3, scutellars 2 per side.

Wings. Similar to male but clavus longer, length of clavus/wing length (including brachiolum) 0.48, extending more than half-way to wing tip.

Legs. General structure similar to male including tarsomeres 4. LR fore 0.7, mid 0.6, hind 0.7. Sensilla chaetica on tarsomere 1, midleg 12, hindleg 7.

Genitalia (Figs 8-10). Gonocoxite not divided into ventrolateral and dorsomedial lobes, but apodeme lobe appears to be present (Fig. 8A); gonocoxapodeme (8B) is dark and slightly curved; coxosternapodeme of IX (8C) dark, prominent and strongly bent; gonocoxite IX closely applied to body with one seta (Figs 8 and 9); coxae small; tergite X with 2 low posterior protruberances each with a long seta (Fig.9). Seminal capsules oval, light brown, with short necks, ducts convoluted with common opening (Fig.10).

PUPA (numerous specimens mounted some with pharate males or females)

As per generic description.

Colour. Greenish in life but occurs in small tent-like light grey tube or cocoon. Exuviae are very light and transparent.

Cephalothorax. Dorsal surface covered with small tubercles; no thoracic horn. Setation: no frontal setae, 2 anteprenotals, 3 small subequal precorneals, two widely spaced dorsocentrals probably representing one member each of the D1,2 and D3,4 pairs.

Abdomen (Figs 11 and 12). Fine shagreen on tergites II-IV and denser, broad anterior bands on V-VIII, no shagreen in conjunctives. Setation as in Fig. 11. Posterior hook rows on tergites III to V and sternites V to VIII. Anal lobe with 3 short macrosetae subterminal and 2 terminal setae, no fringe (Fig. 12).

LARVA (numerous larvae mounted and unmounted)

Similar to generic definition

Colour. Dark green in life with head capsule and posterior claws appearing black.

Body length. Up to 1.5 mm, but difficult to measure as preserved larvae are invariably curved. Head capsule. 300-312 μ m.

Antenna (Fig. 13). AR 0.6, ring organ in basal third of segment 1, blade reaching nearly to base of segment 3, Lauterborn organs and style small.

Labrum (Fig. 14). SI bifid but branches usually closely applied making this difficult to see, pecten epipharynx with 3 subequal teeth, first pair of chaetulae lateralis scalelike, but others large and filmy, fringed with ciliary projections forming part of a filtering apparatus with the modified prementohypopharyngeal complex. Premandible (Fig. 15) with one thin pointed tooth and one broad blunt tooth, without brush.

Mandible (Fig. 16). Teeth dark brown, seta subdentalis pointed, seta interna small with many fine branches.

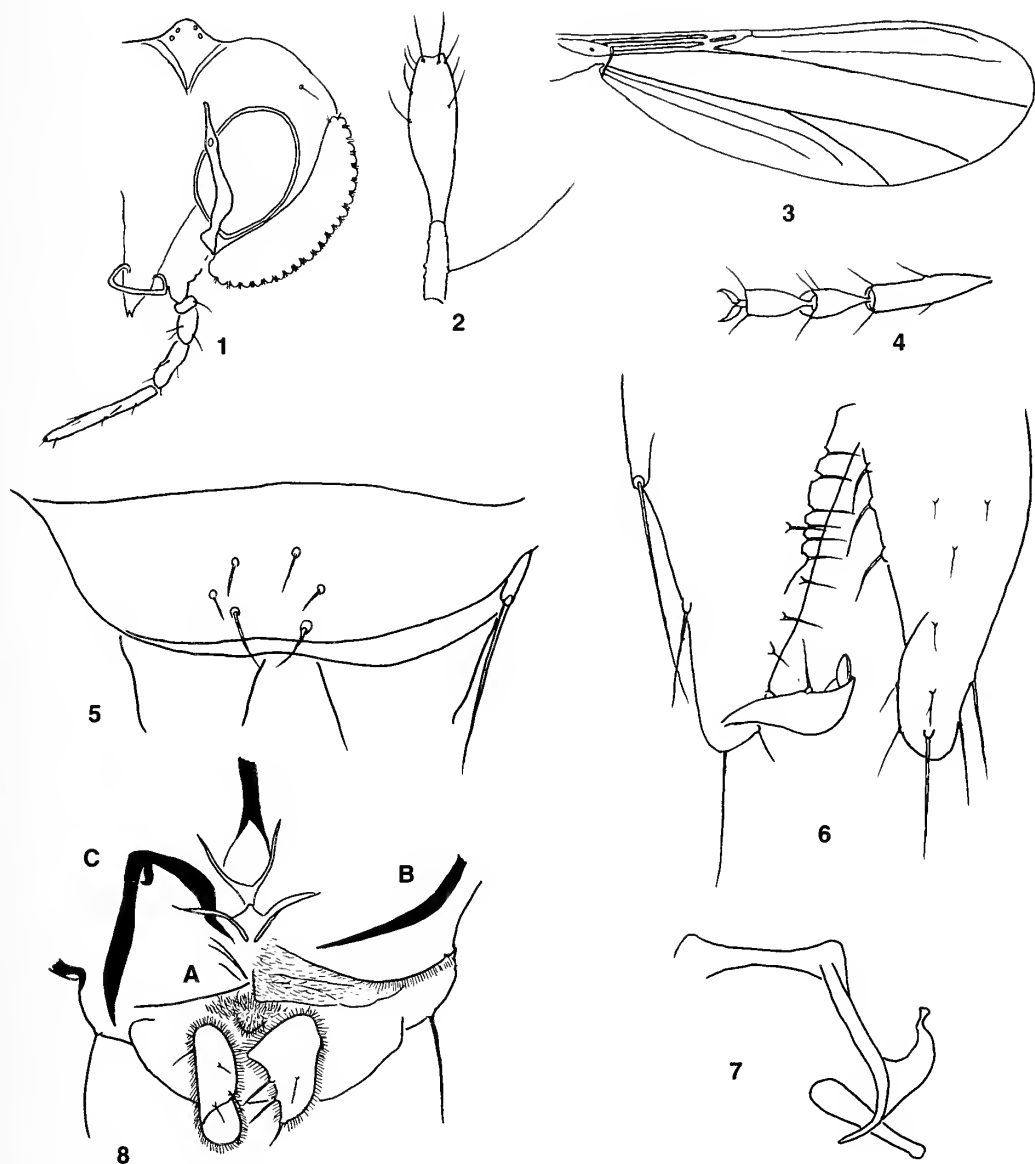
Mentum (Fig. 17). Somewhat elongate, teeth brown, median tooth slightly shorter than first pair of lateral teeth in unworn specimen, ventromental plate distinct but narrow.

Maxilla (Fig 18). As in generic definition.

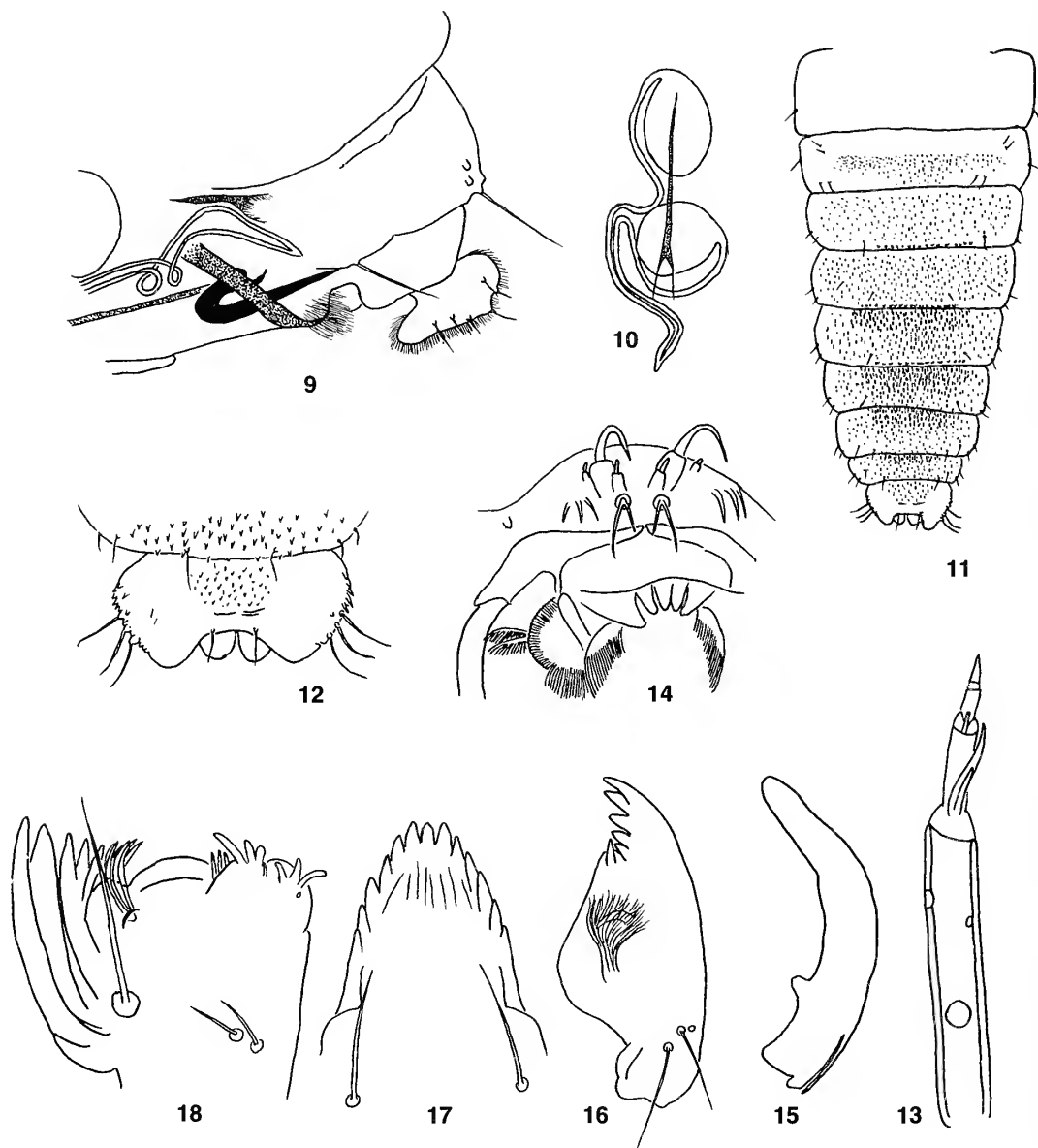
Body. Claws of anterior parapod serrated towards tip, postparapod claws simple, small and dark brown, setae of procercus dark brown, only one pair of small setae in anal region. Body setae appear to be absent.

SPECIMENS EXAMINED. Adults: numerous males and females were netted in the evening or caught in light traps beside the Elands River (33°44'S, 19°06'S), 27.iv.1996, and netted drowned in the Elands River and in the mountain zone of the Riviersonderend (34°03'S, 19°04'E) during ecological work in 1994-95. Numerous pupae and larvae were available from R.Tharme's ecological work in the Elandsrivers, the Dutoitskloof (33°56'S, 19°10'E), the Molenaars (33°43'S, 19°10'E), in the Dutoitskloof Mountains and the mountain zone of the Riviersonderend during 1994-95, all in the Western Cape Province.

Holotype and paratype males, paratype female and pupal and larval material, all mounted on slides, deposited in the Albany Museum, Grahamstown, Eastern Cape Province. COMMENTS. This genus resembles species in the *Corynoneura*-group by the presence of a clavus in the wings of both sexes. According to Sæther and Kristoffersen (1996) there is a distinct sexual dimorphism in the formation of the clavus in the *Corynoneura*-group. In males R_{4+5} plays no part in



Figs 1- 8. *Notocladius capicola*. Adult male: 1. head; 2. antenna, apical flagellomere; 3. wing; 4. tarsomeres 3, 4, 5; 5. anal segment; 6. hypopygium; 7. apodemes. Adult female. 8. genitalia, ventral, A apodeme lobe, B gonocoxapodeme, C coxosternapodeme.



Figs 9 - 18. *Notocladius capicola*. Adult female: 9. genitalia, lateral; 10. seminal capsules and ducts. Pupa: 11. abdomen; 12. anal lobe. Larva: 13. antenna; 14. labrum; 15. premandible; 16. mandible; 17. mentum; 18. maxilla.

its formation but in certain females the base of this combined vein is thickened and in some it is fused to the clavus, as in both sexes of *Notocladius*. These authors consider that the “false vein” arising from the thickened base of R_{4+5} is in reality the extension of this vein and that the additional “false vein” between R_{4+5} and M may represent a vestige of M_1 . Their interpretation can be applied to the wing of *Notocladius* but it is not suggested that this genus falls into the *Corynoneura*-group. This type of wing structure appears to be associated with small body size.

Neglecting wing structure, *Notocladius* keys to somewhere near *Lopescladius* in the key of Cranston *et al.* (1989). The pupae do not fit in anywhere in the key in Coffman *et al.* (1986) but the larvae key into the *Orthocladius-Cricotopus* group in Cranston *et al.* (1983) because of the bifid seta S I and the structure of the mentum. Of course, for practical reasons, keys are based on apomorphic characters which have been developed as a result of ecological specialisation.

ECOLOGY. The tiny larvae and pupae often occur in large numbers on the surface of stones and rocks in the fast current in second or third order mountain streams and rivers in the Western Cape Province. The dark green bodies and almost black head capsules of the free-living larvae make their comma-like appearance most distinctive. They appear to be scrapers but their gut contains very few diatoms, mostly amorphous matter; the filter-like mechanism of their mouth parts should help to gather very small particles scraped off the surface, making them an important part of the food chain. On pupation the larvae make tent-like cases mostly of silk-like fibres incorporating very little detritus, one end is broader than the other and open and presumably faces downstream; no larval remains were found in any of the large number of pupal cases examined.

Adult males swarm at dusk which proved to be a good time to net both males and females; both were also caught in light traps.

So far *N. capicola* has only been found in the soft acid waters of the Table Mountain Sandstone system of the Western Cape Province.

***Parakiefferiella biloba* Freeman**

Eukiefferiella (*Parakiefferiella*) *biloba*, Freeman 1953

Nanocladius biloba, Freeman 1956

Parakiefferiella biloba, Freeman and Cranston 1980

The material studied consists of males, females, pupae, one with mature pharate female, and larvae. Most specimens came from a small mountain stream on the Cape Peninsula which was reduced to a trickle during the dry summer season. The fauna of the stream was very depauperate with very few orthoclad species (including only one species of *Parakiefferiella*, *P. biloba*) being present. It was therefore considered safe to assume that the only larvae of this genus present in a large numbers of samples must be of this species.

Freeman (1953, 1956) describes the male but a more detailed description is given here.

ADULT MALE (N = 5 mounted, numerous species unmounted)

Differs somewhat from the generic definition in Cranston *et al.* (1989).

Body length. 2.00 mm.

Wing length. 1.00 mm.

Colour. Unmounted specimens head, antennae and palps light brown; thorax; scutal stripes and pre-episternum light brown, background and legs yellowish, wings very light brown; abdomen and

hypopygium fairly uniform light brown.

Head. AR 0.17, 12 flagellomeres, 1-3 wider than the rest except for 11 and 12 which form a club, which appears bilobed because of its irregular shape and the prominent groove (Fig. 19), numerous sensilla chaetica on apical flagellomere; no frontal tubercles; eyes bare, small with no dorsal extension, tentorium (Fig. 20) wider ventrally. Head setation: 3 postorbital setae; palp segments 16, 22, 34, 47, 59 μm , 2 subapical sensillae on segment 3, no segment with apical extension.

Thorax. Scutal tuft of microtrichia, diagnostic for the genus, is weak and lies in a small pale patch, but also includes two very small acrostichal setae. Setation: lateral anteprenotals absent, dorsocentrals 9, posterior pre-alars 3, scutellars 2 per side.

Wings (Fig. 21). Similar to Freeman's figures but he does not show that the retracted costa and R veins are thickened; the costa is produced beyond R_{4+5} ; R_{2+3} runs close to R_{4+5} and does not end clearly in the costa. Setation: R 1, R_1 nil, R_{4+5} 1 at tip. There is no anal lobe and one squamal setae (Freeman's specimens had 0 - 2 squamal setae).

Legs. All tarsomeres cylindrical. LR fore 0.9, mid 0.4, hind 0.5. SV fore 2.6, BV fore 2.8. No sensilla chaetica on tarsomeres 1 of midleg and hindleg.

Hypopygium (Figs 22, 23 and 24). Similar to Freeman's figures but he has not shown the virga that is also found in most species of this genus; the small anal point has a large seta on either side (Fig. 22), the inferior volsella is digitiform; the gonostylus (Fig. 23) is not as curved as that illustrated by Freeman but its shape is largely a matter of aspect. The apodemes are shown in Fig. 24.

ADULT FEMALE (N = 5 mounted, many unmounted)

Similar to generic definition in Sæther (1977), except for structure of gonopophysis VIII.

Body length. 1.3 mm.

Wing length. 1 mm.

Colour. Similar to male.

Head. AR 0.5, 5 flagellomeres, last somewhat swollen; no frontal tubercles; eyes similar to male; setation 2 outer verticals, 2 postorbitals. Palp segments 16, 22, 34, 47, 62 μm ; 2 subapical sensillae on segment 3.

Thorax. Scutal patch smaller than that of the male but also with 2 small acrostichal bristles; setation: lateral anteprenotals nil, dorsocentrals 8, posterior pre-alars 3, scutellars 1 or 2 per side.

Wings. Similar to male; setation: brachiolium 1, R 5, R_1 1, R_{4+5} 2, Squama 1 or 2.

Legs. LR fore 0.7, mid 0.4, hind 0.5. No sensilla chaetica on any tarsomeres.

Genitalia (Figs 25, 26 and 27). Gonopophysis VIII divided into a small dorsomesal lobe (Fig. 25 A) and a much larger ventrolateral lobe (Fig. 25 B); the small structure below the dorsomesal lobe in the figure may be an apodeme lobe; gonocoxapodemes light in colour and joined (Fig. 25 C), coxosternapodemes light but prominent (Fig. 25 D); tergite IX with two small posterior protrusions each with one seta; gonocoxite IX welldeveloped with two long and two short setae (Figs 25 and 26), segment X normal, postgenital plate small and rounded, cerci large. Seminal capsules ovoid, brown but with a clearly demarcated light area at junction with spermathecal ducts which are long and convoluted and open close to each other (Fig. 27).

PUPA (N = 3 mounted)

Does not follow generic definition of Coffman *et al.* (1986) in all respects.

Colour. Exuviae are fairly uniform light yellow, shagreen on abdomen darker.

Cephalothorax. Dorsal surface finely pebbled with sculpturing becoming progressively finer laterally. Frontal setae long, not on tubercles (Fig. 28), 2 median anteprenotals, 3 small, short subequal precorneal, 3 dorsocentrals, 1 anterior, and pair posterior; thoracic horn with a few terminal and subterminal spines (Fig. 29).

Abdomen (Fig. 30). Shagreen on tergites I-VII of small posteriorly pointing spines with larger spines forming anterior band and much larger spines forming narrow posterior band, fine, anteriorly pointing spines in conjunctives II-III to VI-VII (Fig. 31); no hook row on II; some short spines on sternites IV-VII. No pedes spurii A or B. Abdominal setation as in Fig. 30, no fringe of taeniate setae on any segment. Anal lobe truncated at apex, not tapering as in other species of this genus; 3 anal macrosetae.

LARVA (N = 5 mounted, many unmounted)

Similar to generic definition in Cranston *et al.* (1983) but differs in some respects

Colour. Head capsule light brown, claws very light, body yellowish when preserved.

Body length. 1.5–2.0 mm.

Head capsule length. 169–195 µm.

Antenna (Fig. 32). AR 0.8; 6-segmented, segment 6 hair-like; blade reaching to base of segment 3 which is very short (1.9 µm) and completely surrounded by large Lauterborn organs, style could not be detected.

Labrum (Fig. 33). SI with 3 branches, remaining S setae simple; no labral lamella; pecten epipharynx of 3 subequal scales; premandible with 2 apical teeth (Fig. 34).

Mandible (Fig. 35). Teeth brown, short apical tooth and 4 inner teeth; seta subdentalis and seta interna both present.

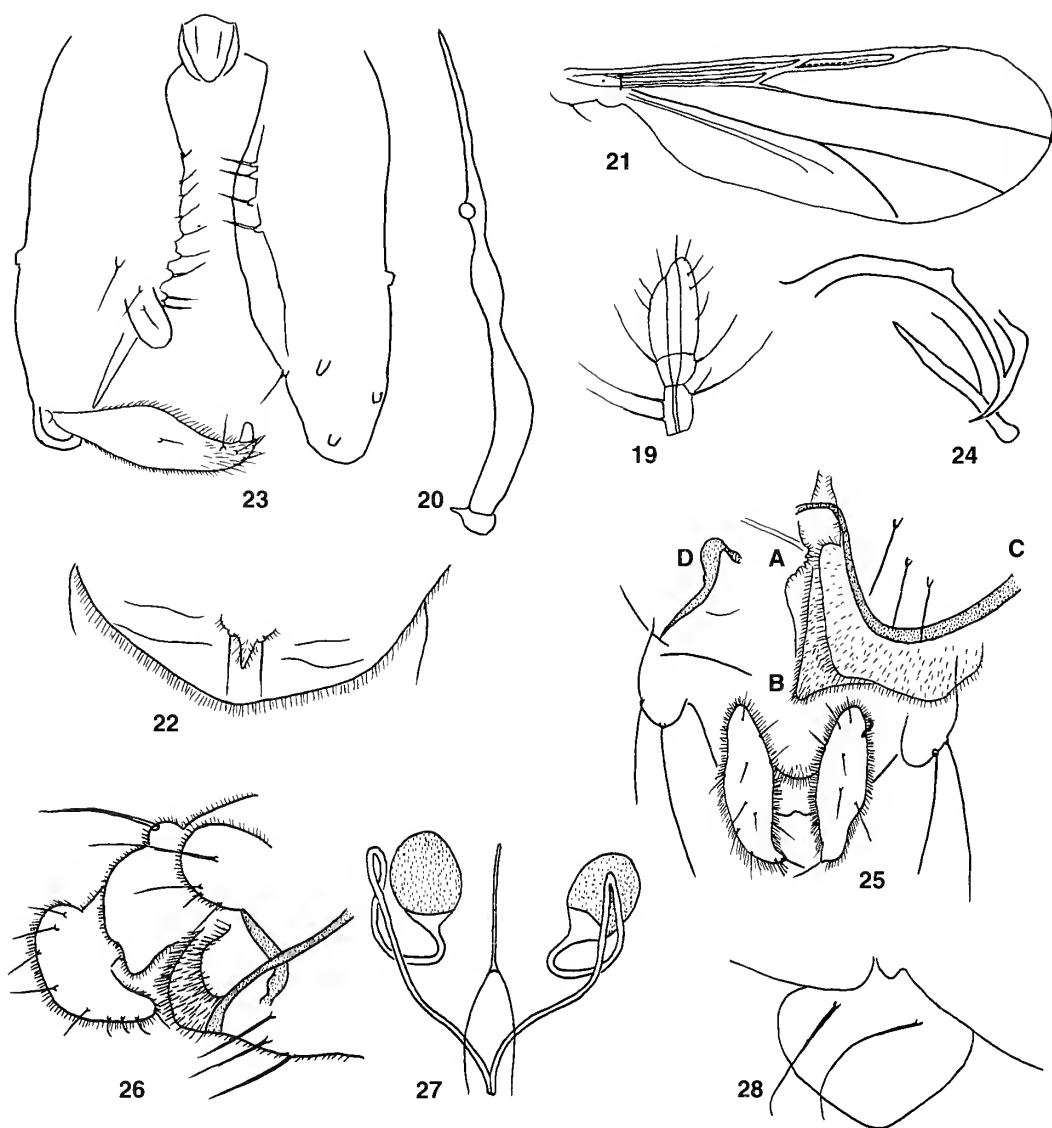
Mentum (Fig. 36, unworn specimen). Teeth brown, 2 median teeth and 5 lateral teeth, there is a sign of an additional lateral tooth adpressed to each median tooth; ventromental plate very small.

Maxilla (Fig. 37). Palpiger normal with numerous small lamellae at base, mostly behind the palpiger in the figure; a pecten galearis could not be detected; the base of an antaxial seta present but no seta; seta maxillaris simple.

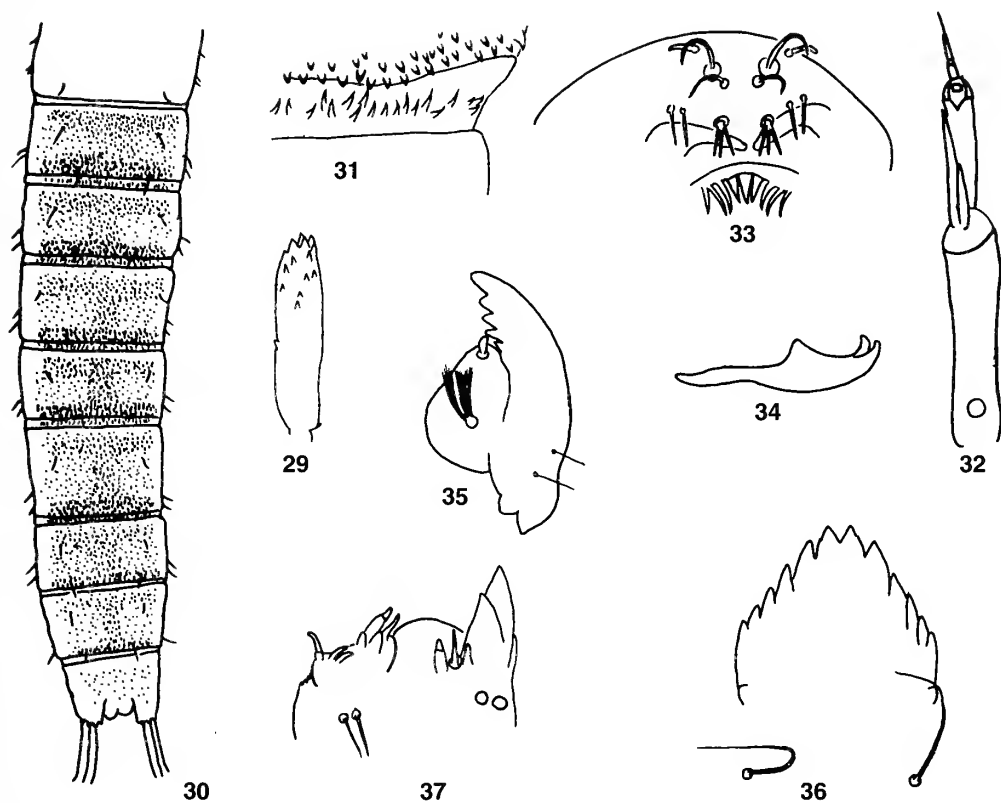
Body. Parapods normal; procercus 2x as long as wide with 8 long setae; some simple body setae up to 62 µm long; anal tubules shorter than parapod and somewhat conical in shape.

SPECIMENS EXAMINED. Adults: numerous males and females from small waterfall, tributary of Silvermine River, Cape Peninsula, 10 and 11.xi.1995, 24.ii.1995, 1.xii.1995, 9.i.1996; 1 female, Kalk Bay waterfall, Cape Peninsula, 20.xii.1994; numerous males and females, Elands River, Du Toit's Kloof (33°44'S, 19°06'E), 27.iv.1996; 1 male upper Riviersonderend (34°03'S, 19°04'E), 8.iv.1995. Pupae: small waterfall, tributary of Silvermine River 2 exuviae 24.xi.1995, 1 pupa with pharate female 1.xii.1995. Larvae: numerous from the tributary of Silvermine River at dates above.

COMMENTS. The adult male, pupa and larva all differ from the generic definitions to some extent; the male in that it has small acrostichal setae in the thoracic tuft of microsetae, the squama of the wing is not bare; the pupa in that the anal lobes are truncated at the apex and not extended into tails; the larvae in that the Lauterborn organs of the antennae are large and not small and the antennal style is absent or much reduced and not strong. There are a few other minor differences, but none seem to warrant a new genus being erected. It should be noted that neither the male nor the female adult has the apical projection on palp segments as seen in the African species discussed by Ferrington and Sæther (1995).



Figs 19- 28. *Parakiefferiella biloba*. Adult male: 19. flagellomeres 11 and 12; 20. tentorium; 21. wing; 22. anal point; 23 hypopygium; 24 apodemes. Adult female. 25. genitalia, ventral, A dorsomesal lobe, B ventrolateral lobe, C gonocoxapodeme, D coxosternapodeme; 26 genitalia, lateral; 27. seminal capsules and ducts. Pupa: 28. frontal setae.



Figs 29 - 37. *Parakiefferiella biloba*. Pupa: 29 thoracic horn; 30. abdomen; 31. conjuncture II-III. Larva. 32. antenna; 33. labrum; 34. premandible; 35. mandible; 36. mentum; 37. maxilla.

ECOLOGY. *P. biloba* is found in first or second order mountain streams and small rivers. The larvae from the small waterfall were inhabiting the moss and *Scirpus digitatus* in the water flow.

DISTRIBUTION. Cape Peninsula mountains. Western Cape Province Fold Belt Mountains and source streams of the Tugela River, Drakensberg Mountains, KwaZuluNatal.

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**Phylogenetic Systematics of the Family Teloganodidae
(Ephemeroptera: Pannota)**

W. P. MCCAFFERTY and T. Q. WANG

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Phylogenetic Systematics of the Family Teloganodidae (Ephemeroptera: Pannota)

by

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West Lafayette, IN 47907 USA)

ABSTRACT

Teloganodidae **stat. nov.** is recognized at the family rank and shown to be a sister group to Ephemerellidae. Cladistic analysis of monophyletic species groups was performed, and the most parsimonious cladogram is presented and discussed in terms of evolutionary trends and instances of homoplasy. There are two major clades; these are recognized as the subfamilies Austremerellinae **subfam. nov.** and Teloganodinae. Genera are defined cladistically by autapomorphies, and sequencing conventions within the context of a strictly phylogenetic classification allow their recognition at this rank. Two genera are recognized in Austremerellinae: *Austremerella* from Australia and *Vietnamella* from southeastern Asia. Six genera are recognized in the Teloganodinae: *Ephemerellina*, *Nadinella* **gen. nov.**, *Lithogloea*, and *Lestagella* from southern Africa, and *Macafertiella* and *Teloganodes* from southern Asia. Previous interpretations of *Austremerella* and *Lithogloea* as subgenera of *Ephemerellina* were based on symplesiomorphies and are untenable. Each genus is distinctive in both larval and adult stages, and a stage-correlated key is provided. Descriptive and geographic accounts for each higher taxon are given, and known species listed. The new genus *Nadinella* contains two nominal species: *N. crassi* (Allen and Edmunds) **comb. nov.** and *N. brincki* (Demoulin) **comb. nov.** Australian and South African genera are shown to be archaic phylogenetic relicts with origins in Gondwanaland prior to the initial breakup of that landmass. It is hypothesized that the presence of Oriental lineages has resulted from Australasian interchange in the case of Austremerellinae, and Africa to Asia transport via the Indian subcontinent in the case of Teloganodinae.

INTRODUCTION

The family Teloganodidae **stat. nov.** is a group of pannote mayflies (McCafferty and Edmunds 1979) known from South Africa, the Orient, and Australia. These mayflies have not been generally well known in the past, and incomplete and sometimes erroneous information has resulted in a history of divergent interpretations. There are only 15 species currently described in the Teloganodidae. This may in part be attributed to the relict nature of the older Gondwanan element of the family; however, we anticipate that several more will be described from the more recent Oriental fauna within the family. For example, we know of at least five undescribed species from southeast Asia at this time.

The ecology of Teloganodidae is poorly known. Available collecting data, however, indicate that larvae of all genera are restricted to mountain streams and rivers where they occur on stones or vegetation in mostly swift currents. Our collecting records from South Africa, Sri Lanka, and Borneo indicate that teloganodid larvae are commonly found on the vertical substrates of waterfalls. Thus, an appropriate vernacular name for the family would be "the waterfall mayflies." Harrison and Agnew (1962) found that certain of the South African teloganodids were restricted to acid waters and gave

some additional ecological data. The only gut sample study (Tshernova 1972) indicates that the larvae of the Oriental *Vietnamella* Tshernova are periphyton feeders. Differences we have found in development of filtering setae on mouthparts of different genera, however, suggest that teloganodid larvae may also be fine detritus collectors to various degrees. McShaffrey and McCafferty (1990a, 1990b) found a considerable range of feeding behavior in certain members of the related family Ephemerellidae. The fact that Barnard (1932) has also reported teloganodid larvae from under stones suggests detritus deposit feeding. According to Barnard (1932), some teloganodid larvae crawl out of the water prior to emerging to the subimago, although it is not known if this is facultative or obligatory behavior, or if it is widespread among species. Edmunds and McCafferty (1988) noted that such behavior is predominant in primitive extant mayflies.

We will show that the Teloganodidae is a monophyletic lineage, and is a sister group to the larger, generally more well known, and more apotypic Holarctic and Oriental family Ephemerellidae, within which it was previously considered a subfamily (Allen 1965). Our conclusions are based on the phylogenetic data we present herein. Furthermore, our linear higher classification of Teloganodidae into subfamilies and genera is completely congruent with our cladistics data, in that it is strictly phylogenetic and permits reproduction of the deduced cladogram of the taxa, as was advocated by McCafferty (1991a).

The original concept of the family Ephemerellidae dates to Eaton (1883-88) with his Section 6 of *Ephemerella*, which included the Holarctic and Oriental genus *Ephemerella* Walsh and Oriental genus *Teloganodes* Eaton, as they were known at that time. Klapálek (1909) first used the family rank designation, but included only *Ephemerella*. Ulmer (1920) added the South American genus *Melanemerella* Ulmer to the family, and Lestage (1924) added the South African genus *Ephemerellina* Lestage. Various other genera were described in the family up to the time that Edmunds and Traver (1954), in their outline of higher reclassification, included the following world genera in the Ephemerellidae: *Ephemerella*, *Ephemerellina*, *Lithogloea* Barnard (South Africa), *Melanemerella*, *Teloganella* Ulmer (Oriental), *Teloganodes*, and *Teloganopsis* Ulmer (Oriental).

Demoulin (1955) removed *Melanemerella* from the family Ephemerellidae and placed it in a new subfamily Melanemerellinae of Tricorythidae, and Edmunds et al. (1963) recognized this subfamily but returned it to Ephemerellidae. Wang and McCafferty (1996a) recently removed *Melanemerella* from Ephemerellidae by demonstrating that it is not a member of the Pannota but probably an aberrant member of Leptophlebiidae.

Allen (1965) erected the subfamily Teloganodinae within the Ephemerellidae and included in it the genera *Teloganodes* and *Ephemerellina*. He considered *Austremerella* Riek, from Australia, to be synonymous with *Ephemerellina*; he did not mention *Lithogloea*. Demoulin (1970) described the South African genus *Lestagella* Demoulin in the Ephemerellidae, but did not place it any subfamily. He also placed *Lithogloea* as a subgenus of *Ephemerellina*. Tshernova (1972) described the Oriental genus *Vietnamella* in the family Ephemerellidae, and although Allen (1980, 1984) placed this genus in the Ephemerellinae, Edmunds and Murvosh (1995) correctly recognized that it belonged to the Teloganodinae. Furthermore, Wang and McCafferty (1995) showed that those Oriental species placed in *Ephemerellina* (Allen and Edmunds 1963a, Tshernova 1972) are in actuality species of *Vietnamella*. Allen (1973) described the genus *Manohyphella* Allen from Madagascar and added it to the Teloganodinae along with *Teloganella*. Although never stated by Allen, *Lestagella* was also, by default, considered in the subfamily Teloganodinae, because he did not include it in Ephemerellinae (Allen 1980, 1984).

In 1990, Hubbard listed the following genera in Teloganodinae: *Ephemerellina*, *Lestagella*, *Manohyphella*, *Teloganella*, and *Teloganodes*. Since then, Wang et al. (1995) have removed *Teloganella* from the Teloganodinae and Ephemerellidae, showing that it is instead a member of the family Tricorythidae. Its classification previously had been argued by Edmunds and Polhemus (1990) and Peters and Peters (1993), but neither paper offered any supporting data. McCafferty and Wang (1995) have also removed *Manohyphella* from Ephemerellidae and Teloganodinae, showing that it also is a member of the Tricorythidae. McCafferty and de Moor (1995) re-established the genus *Lithogloea*, thus adding it to the Teloganodinae. As mentioned above, *Vietnamella* was shown to be a member of Teloganodinae (Edmunds and Murvosh 1995). Finally, the Sri Lankan genus *Macafertiella* Wang was recently described in Teloganodinae by Wang and McCafferty (1996b).

Taking into account the complex history of the group, and the results of our cladistic analysis, we recognize herein the following genera in the family Teloganodidae: *Austremerella*, *Ephemerellina*, *Lestagella*, *Macafertiella*, *Nadinella* **gen. nov.** from South Africa, *Teloganodes*, and *Vietnamella*. The entire higher classification is shown in Table 1. We will show that the previous synonymies of *Austremerella* with *Ephemerellina*, and *Lithogloea* with *Ephemerellina* were essentially based on symplesiomorphies.

TABLE 1. Higher classification and general distribution of the Teloganodidae

Family Teloganodidae
Subfamily Austremerellinae subfam. nov.
Genus <i>Austremerella</i> (Australian)
Genus <i>Vietnamella</i> (Oriental)
Subfamily Teloganodinae
Genus <i>Ephemerellina</i> (Southern Afrotropical)
Genus <i>Nadinella</i> gen. nov. (Southern Afrotropical)
Genus <i>Lithogloea</i> (Southern Afrotropical)
Genus <i>Lestagella</i> (Southern Afrotropical)
Genus <i>Macafertiella</i> (Oriental)
Genus <i>Teloganodes</i> (Oriental)

The extensive material that we have been able to bring together for comparative analysis has been of vital importance in unravelling the systematics of this group. In particular, this has included Oriental material donated from the George F. Edmunds, Jr. collection (including a recent gift from T. Soldán from Vietnam), previously held at the University of Utah and now held in the Purdue Entomological Research Collection (PERC herein), West Lafayette, Indiana; Australian material loaned and donated by the Australian CSIRO (Australian National Collection, or ANC herein); South African material loaned by the Albany Museum (AM herein); and the extensive material collected in South Africa by the first author and Nadine McCafferty in 1990. The latter and donated material resides in PERC.

Resolving the generic classification and assignment of species and stages in southern Africa (where we recognize four endemic genera) was especially challenging. This was due to numerous factors. Many species were originally incompletely described or characteristics were not described accurately. Some species were subsequently misidentified in the literature, and larval and adult stages were not always associated correctly. Some geographic records attributed to African teloganodines proved to be misidentifications of tricorythid mayflies. We were able to recognize erroneous stage correlations by employing a method discovered and used by McCafferty and Wang (1994) wherein it was shown that the position and relative development of larval structures, such as tubercles, other

cuticular processes, and gills, can be represented in the adult stage by recognizable vestiges or associated vestiges (e.g., gill socket vestiges). As an example, we demonstrate that adults assigned to *Ephemerellina barnardi* Lestage by Barnard (1940) were misidentified and do not match adults correctly assigned by him to this species earlier (Barnard 1932). Moreover, the misidentified adults can be associated with larvae originally described as *Ephemerellina crassi* Allen and Edmunds (1963a), which is the type of our new genus *Nadinella*. True larvae of *E. barnardi* were part of the original series of larvae that had been incorrectly associated by Barnard (1932) with *Lithogloea harrisoni* Barnard.

Although our higher classification of the Teloganodidae (Table 1) is based on results of our phylogenetic research, which is essentially represented by a cladogram of species groups, we present the cladistic methods, analysis, and discussion following presentation of the taxonomic keys and systematic accounts of the taxa. The Key to Genera we present is a stage-associated key, meaning that larvae and adults of each genus ideally are keyed together at the same place and in the same sequence in the key. For each genus in the Accounts of Taxa, we give a generic synonymy and type species, descriptions of larval and adult stages, diagnostic information, species included with specific synonymies, distribution, material examined, and remarks regarding systematics and ecology. In addition, 90 morphological figures, including a dorsal whole larval habitus of each genus, are included.

ACCOUNTS OF TAXA

Family Teloganodidae stat. nov.

DESCRIPTION OF MATURE LARVAE

Eyes dorsal or dorsolateral (Figs 2-10), those of males (Figs 4, 10) divided into two distinct parts. Mouthparts more or less prognathous, with branched, hairlike setae present, with variously sized setules (e.g., Figs 47-64); labium relatively small. Forewingpads (Figs 2-10) fused with mesonotum for most of their length, not juxtaposed posteriorly; posterior margin of mesonotum between apices of wingpads with well-developed submedial lobes and medial V-shaped emargination. Hindwingpads present. Simple, filamentous gills absent or present laterally on abdominal segment 1; lamellate gills (Figs 2-10) dorsal and present on abdominal segments 2-5, 2-6, or 2-7; gills on abdominal segment 2 operculate (Figs 7-10), semi-operculate (Figs 4-6), or not operculate (Figs 2, 3); when gills on abdominal segment 2 operculate or semi-operculate, then such gills more or less elongate-rounded and always well separated from each other. Median caudal filament developed (three tailed) (Figs 2-7) or reduced and rudimentary (two tailed) (Figs 8-10).

DESCRIPTION OF ADULT

Eyes of male each divided into two distinct parts. Forewings (Figs 80-87) usually with many short, detached, marginal intercalaries (Figs 80, 83-87) or sometimes with most short intercalaries attached (often to crossveins) (Figs 81, 82); one to four main CuA intercalaries present. Hindwings present. Abdominal segment 2 with gill socket vestiges (Fig. 89). Male genitalia (Figs 90, 91) with three segmented forceps; forceps segment 1 relatively long, more than twice as long as wide. Median caudal filament developed (three tailed) or reduced (two tailed).

DIAGNOSIS OF THE FAMILY

The Teloganodidae is distinct from other families of pannote mayflies. Larvae are distinguished from the Ephemerellidae by the presence of gills on abdominal segment 2. They differ from other families of Pannota with gills on abdominal segment 2 (e.g., Leptohyphidae, Tricorythidae, Caenidae) by the posterior aspect of the mesonotum that has submedian lobes and a V-shaped median notch, and by the subdivided eyes of the mature (pharate) males. Adults of Teloganodidae share generalized, ancestral wing venation and derived divided male eyes with the Ephemerellidae, but differ from them with respect to their distinctly more elongate basal segment of the male genital forceps. All adults of Teloganodidae can be told from all adults of Ephemerellidae by possession of gill socket vestiges on abdominal segment 2. The adults can be told from other pannote mayflies by their general cubital venation, and, with the exception of Ephemerithus (Tricorythidae), by the presence of short marginal intercalaries along the outer margin of the forewings.

KEY TO GENERA

(Couplets 2-4 pertain to genera known from Australia and the Orient; couplets 5-7 pertain to genera known from southern Africa)

1. Larva: Gills present on abdominal segment 7; gills on abdominal segment 2 not operculate or semi-operculate (Figs 2, 3).
Adult: Forewings (Figs 80-82) with stigmatic costal interspace divided by secondary longitudinal vein into upper and lower series of many cellules.
.....Subfamily Austremerellinae, 2
- Larva: Gills absent on abdominal segment 7; gills on abdominal segment 2 operculate or semi-operculate (Figs 4-10).
Adult: Forewings (Figs 83-87) with stigmatic costal interspace not divided into upper and lower series of many cellules.
.....Subfamily Teloganodinae, 3
2. Larva: Head (Fig. 3) with pair of prominent, elongate, anteriorly directed cephalic horns originating anterior to eyes; forefemora (Fig. 3) very broad and denticulate anteriorly.
Adult: Mesothorax without pair of long membranous processes posteriorly; head with cephalic horn vestiges; forewings (Figs 81, 82) with most marginal intercalaries basally attached.
.....Genus *Vietnamella*
- Larva: Head (Fig. 2) without pair of cephalic horns; forefemora (Fig. 2) not as above.
Adult: Mesothorax (Fig. 88) ending posteriorly with pair of narrow-elongate, membranous processes; head without cephalic horn vestiges; forewings (Fig. 80) with most marginal intercalaries not attached basally.
.....Genus *Austremerella*
3. Larva: Two tailed, with median caudal filament reduced (Figs 8-10).
Adult: Two tailed, with median caudal filament reduced.
.....4
- Larva: Three tailed, with well-developed median caudal filament (Figs 4-7).
Adult: Three tailed, with well-developed median caudal filament.
.....5
4. Larva: Gills present on abdominal segment 6; median row of dorsal abdominal tubercles well developed (Fig. 8), with tubercle on tergum 10 longer than that of tergum 3.
Adult: Unknown; distribution may be limited to Sri Lanka.
.....Genus *Macafertiella*

- Larva: Gills absent on abdominal segment 6; median row of tubercles absent (Fig. 10) or only poorly developed (Fig. 9), with tubercle on tergum 10, when present, shorter (Figs 9, 10) or longer than that of tergum 3.

Adult: Not comparable because adult of *Macafertiella* unknown; generally distributed in Southeast Asia from India to Philippines.

.....Genus *Teloganodes*

5. Larva: Lamellate gills present on abdominal segments 2-5; claws (Fig. 71) with two rows of denticles; abdomen with pairs of dorsal tubercles (Figs 5, 74, 76) or broad, straight-margined or slightly bifurcated posteromedial protuberances (Figs 75, 76) on at least some terga.

Adult: Abdominal terga 2-5 with gill socket vestiges; terga 3-5 each with small, broad thickening medially, usually with two minute tubercles, or without apparent tubercle vestiges; if tubercle vestiges absent, then IMP of forewings longer than MP_2 and both directly attached to each other (Fig. 84).

.....Genus *Nadinella* gen. nov.

- Larva: Lamellate gills on abdominal segments 2-4 or 2-6; claws (Figs 70, 72, 73) with one row of denticles; abdomen (Figs 4, 6, 7) without paired or broad, straight-margined or bi-lobular, posteromedial dorsal tubercles or protuberances.

Adult: Abdominal terga 2-4 or 2-6 with gill socket vestiges; terga 3-5 (or more) with no dorsal tubercle vestiges or with only single median tubercle vestige; if tubercle vestiges absent, then IMP of forewings shorter than MP_2 and basally detached from MP_2 (Fig. 86).

.....6

6. Larva: Head (Fig. 7) margined with long setae anteriorly; gills on abdominal segment 2 (Fig. 7) operculate.

Adult: Abdominal segment 5 without gill socket vestiges; IMP of forewings shorter than MP_2 (Fig. 86).

.....Genus *Lestagella*

- Larva: Head (Figs 4, 6) not margined with long setae; gills on abdominal segment 2 (Figs 4, 6) semi-operculate, with part of following gill pair exposed.

Adult: Abdominal segment 5 with gill socket vestiges; IMP of forewings shorter (Fig. 85) or longer (Fig. 83) than MP_2 .

.....7

7. Larva: Abdomen (Fig. 4) with median dorsal row of sharp tubercles; Gills absent on abdominal segment 1.

Adult: Abdominal terga 3-6 (Fig. 89) each with small, median tubercle vestige; IMP of forewings longer than MP_2 , and MP_2 attached directly to IMP (Fig. 83).

.....Genus *Ephemerellina*

- Larva: Abdomen (Fig. 6) with single median row of dorsal tubercles represented by broad-based and attenuated extensions of the posterior tergal margins; Gills present on abdominal segment 1.

Adult: Abdominal terga 3-6 without tubercles; IMP of forewings shorter than MP_2 and detached from it (Fig. 85).

.....Genus *Lithogloea*

Subfamily Austremerellinae subfam. nov.

DIAGNOSIS

Larvae of the Austremerellinae may be told from those of the Teloganodinae by the presence of gills on abdominal segment 7 (Figs 2, 3). Gills on abdominal segment 2 are not operculate or semi-

operculate in Austremerellinae (Figs 2, 3). The inner margins of the cerci have elongate, relatively dense, and sometimes forked, hairlike setae along the medial margin (Figs 77, 78). Larvae of Austremerellinae also possess a double row of small, sharp tubercles on abdominal terga (Figs 2, 3), whereas only in the South African genus *Nadinella* **gen. nov.** can a double row of tubercles be found in the Teloganodinae, and these tend to be blunt. Adults of Austremerellinae possess forewings with a complex stigmatic area, being longitudinally subdivided by a secondary vein into extensive upper and lower rows of cellules between the Costa and Subcosta (Figs 80-82). Forewings of Austremerellinae also have more elongate intercalary veins in that area between IMP and CuA, and have three or more CuA intercalary attachments to CuA. Adults also possess gill socket vestiges on abdominal segment 7, although they may be difficult to discern.

Genus *Austremerella* Riek

(Figs 2, 11, 20, 29, 38, 47, 56, 77, 80, 88)

Austremerella Riek, 1963:50. (Larva and adult) Type: *Austremerella picta* Riek, by original designation.

Ephemerellina (subgenus *Austremerella*), Allen, 1965:264.

DESCRIPTION OF MATURE LARVA

Head (Fig. 2) without cephalic horns. Labrum (Fig. 11) subquadrate, approximately twice as broad as long, with short, scattered setae over entire dorsal surface. Mandibles (Figs 20, 29) robust; incisors oriented distally; medioapical setal patch of setae developed on left mandible (Fig. 29). Maxillae (Fig. 38) with palpi absent. Superlinguae of hypopharynx (Fig. 47) moderately developed, slightly concave laterally and not extending beyond lingua distally; apical margin of lingua convex. Labium (Fig. 56) with well-divided and apically narrowed glossae and paraglossae; palpal segment 3 longer than width of segment 2. Pronotum (Fig. 2) short, more than twice as broad as long, not produced anterolaterally. Forefemora (Fig. 2) moderately broad. Tarsal claws with one row of denticles. Simple filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-7; gills on abdominal segment 2 (Fig. 2) not operculate or semi-operculate. Paired dorsal abdominal tubercles present (Fig. 2). Caudal filaments not banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Head without pair of cephalic horn vestiges. Mesothorax ending posteriorly with pair of elongate membranous processes (Fig. 88). Forewings (Fig. 80) with IMP longer than MP_2 ; MP_2 attached directly to IMP; most marginal intercalaries free, not attached. Abdominal segments 2-7 with gill socket vestiges. Median caudal filament well developed (three tailed).

DIAGNOSIS

The larvae of *Austremerella* can be distinguished from those of *Vietnamella* by their lack of cephalic horns, maxillary palpi, and gills on abdominal segment 1. Furthermore, segment 3 of the labial palpi are much longer; the mandibles are not modified apically as in *Vietnamella* (Figs 21, 30); and the labrum of *Austremerella* has short setae scattered over the entire dorsal surface, whereas in *Vietnamella*, the setae are confined to the distal half of the dorsal surface of the labrum. The adults

of *Austremerella* have a unique pair of membranous filaments as described above, and most marginal intercalary veins in the forewings are typical of the family and also Ephemerellidae, in that they are unattached. Most short marginal intercalaries of the forewings of *Vietnamella* are attached to other veins.

SPECIES INCLUDED

Austremerella picta Riek
Austremerella picta Riek, 1963:50.
Ephemerellina picta (Riek), Allen, 1965:264.

DISTRIBUTION

Australia: Queensland.

MATERIAL EXAMINED

Austremerella picta: AUSTRALIA: Larvae, Queensland, Flaggy Cr., Mistake Mtns. via Laidley, S. E. Old, II-11-1973, S. R. Monteith, ANC, PERC. Female adult paratype, Queensland, Lamington Natl. Park, VIII-11-1942, E. F. Riek, PERC.

REMARKS

This monotypic genus is defined by the following autapomorphies (see also Phylogenetics, below): the elongation of labial palpal segment 3, and the presence of unusual mesothoracic processes in the adults. Within the subfamily Austremerellinae, they are further defined by loss of the gills on abdominal segment 1 and the loss of maxillary palpi. Otherwise, the genus appears to be the most plesiotypic genus within the family (with the possible exception of *Ephemerellina* of the subfamily Teloganodinae), retaining a preponderance of plesiomorphic character states. Riek (1963) did not notice the pair of gills on abdominal segment 7 of the larvae, and this led to some historical confusion about the integrity of the genus. Allen (1965) incorrectly considered it a subgenus of *Ephemerellina*. The male adults of *A. picta* remain unknown. Above, we provide new collecting data associated with the larvae. Unfortunately, the only ecology known of *Austremerella* is that larvae have been found in mountain streams.

Genus *Vietnamella* Tshernova

(Figs 3, 12, 21, 30, 39, 48, 57, 69, 78, 81, 82)

Vietnamella Tshernova, 1972:366. (Larva) Type: *Vietnamella thani* Tshernova, by original designation.

Vietnamella, You and Su, 1987:176. (Adult).

Vietnamella, Wang and McCafferty, 1995:193. (Revision).

DESCRIPTION OF MATURE LARVA

Head (Fig. 3) with prominent, anteriorly directed cephalic horns anterior to eyes. Labrum (Fig. 12) with lateral margins convergent distally, approximately twice as broad as long, with scattered

moderately long setae in distal half dorsally. Mandibles (Figs 21, 30) narrow basally, broad apically; incisors fused and oriented more or less laterally; medioapical patch of setae developed on left mandible. Maxillae (Fig. 39) with three-segmented palpi. Superlinguae of hypopharynx (Fig. 48) moderately developed, rounded laterally, and slightly shorter than lingua; apical margin of lingua straight. Labium (Fig. 57) with short and broad, apically truncate glossae and paraglossae; palpal segment 3 very short, with length less than width of segment 2. Pronotum (Fig. 3) about 1.5 times as broad as long, anterolateral corners produced into processes. Tarsal claws (Fig. 69) with one denticle. Simple, filamentous gills present on abdominal segment 1; lamellate gills present on abdominal segments 2-7; gills on abdominal segment 2 (Fig. 3) not operculate or semi-operculate. Paired dorsal abdominal tubercles present (Fig. 3). Caudal filaments not banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Head with pair of cephalic horn vestiges. Mesothorax without pair of elongate membranous processes. Forewings (Figs 81, 82) with IMP nearly as long as MP₂; MP₂ attached to IMP near base; most short marginal intercalaries are attached to crossveins or longitudinal veins. Abdominal segments 2-7 with gill socket vestiges. Median caudal filament well developed (three tailed).

DIAGNOSIS

The larvae of *Vietnamella* can be distinguished from those of *Austremerella* by the presence of cephalic horns, restricted setae on the labrum, fused and laterally oriented incisors on the mandibles, maxillary palpi, the shorter terminal labial palpal segments, the truncate glossae and paraglossae, the longer prothorax, the single denticle of the tarsal claws, and gills on abdominal segment 1. The adults of *Vietnamella* have vestiges of the larval cephalic horns on the head, and they do not have the specialized mesothoracic filaments present in *Austremerella*.

SPECIES INCLUDED

- Vietnamella dabieshanensis* You and Su
- Vietnamella dabieshanensis* You and Su, 1987:176.
- Vietnamella guadunensis* Zhou and Su, 1995:48.
- Vietnamella ornata* (Tshernova)
- Ephemerellina ornata* Tshernova, 1972:368.
- Vietnamella ornata* (Tshernova), Wang and McCafferty, 1995.
- Vietnamella qingyuanensis* Zhou and Su, 1995:47.
- Vietnamella sinensis* (Hsu)
- Ephemerella sinensis* Hsu, 1936:325.
- Ephemerellina sinensis* (Hsu), Allen and Edmunds, 1963a:15.
- Vietnamella sinensis* (Hsu), Wang and McCafferty, 1995:193.
- Vietnamella thani* Tshernova
- Vietnamella thani* Tshernova, 1972:367.

DISTRIBUTION

The genus is known from Vietnam and southern and southeastern China (Yunnan, Anhui, Fujian, Jiang Xi, and Zhejiang Provinces).

MATERIAL EXAMINED

Vietnamella thani: VIETNAM: Larvae, Vinh Phu Prov., R. Dan, Tran Dao, X-17-1984, T. Soldán, PERC.

REMARKS

This genus is defined by the following autapomorphies (see also Phylogenetics, below): the presence of cephalic horns in the larvae (including their vestiges in the adults), the laterally oriented, fused mandibular incisors, the apically truncate paraglossae, the single claw denticle, and the fact that most short marginal intercalaries in the forewings are attached either to crossveins or longitudinal veins. The relatively large number of autapomorphies of *Vietnamella* shows that it is a relatively apotypic genus within an old subfamily. It is phenetically so different from other teloganodids that we consider it aberrant. It is not surprising that all workers previous to Edmunds and Murvosh (1995) considered it in Ephemerellidae (Ephemerellinae). Wang and McCafferty (1995) showed that all Oriental species that were previously known as adults and that were called *Ephemerellina* were in fact *Vietnamella*. The taxonomy of species is somewhat dubious at the present because species have not been adequately compared with each other. For example, the known alate forms of *V. ornata* (unknown as larvae) may prove to be associated with the larvae of *V. thani* (unknown in alate stages). In addition, *V. sinensis* and *V. dabieshanensis* have been taken from the same general area in the Dabie Mountains of southeastern China, and they might prove to be synonymous, and Zhou (pers. comm.) has indicated that he believes that *V. guadunensis* and *V. qingyuanensis* are actually immature *V. dabieshanensis*.

Little is known of the habitat or habits of this genus, although Tshernova (1972) indicated that the larvae of *V. thani* were periphyton feeders. Adaptive convergences in mouthpart structure found in *Vietnamella* and the genera *Lestagella* and *Teloganodes* of the subfamily Teloganodinae (reduced mandibles, and well-developed filtering setae marginally on the labrum, on short superlinguae, and on paraglossae and somewhat fused glossae) suggest that there are close feeding similarities, including filtering ability in the three genera.

Subfamily Teloganodinae

DIAGNOSIS

Larvae of the Teloganodinae may be distinguished from those of the Austremerebellinae by the absence of gills on abdominal segment 7, by the presence of either operculate (Figs 7-10) or semi-operculate (Figs 4-6) gills on abdominal segment 2, and their shorter and more sparsely setaceous cerci (Fig. 79). All larvae lack maxillary palpi (Figs 40-46) and tubercles or horns on the head (Figs 4-10). Also, larvae either possess a double row of blunt tubercles (Figs 5, 74-76), a single row of sharp or blunt tubercles (Figs 4, 6, 8, 9), or no dorsal tubercles (Figs 7, 10) on the abdominal terga. Adults of Teloganodinae do not have a forewing stigmatic area that is divided by a secondary longitudinal vein into two rows of several cellules, and there are fewer intercalary veins between IMP and CuP (Figs 83-87). They also lack gill socket vestiges on abdominal segment 7 (Fig. 89).

Genus *Ephemerellina* Lestage

(Figs 4, 13, 22, 31, 40, 49, 58, 65, 70, 79, 83, 89)

Ephemerellina Lestage, 1924:346. (Adult). Type: *Ephemerellina barnardi* Lestage, by original designation.

Ephemerellina, Barnard, 1932:251. (Larva).

Ephemerellina, Allen, 1965:293. (Incl. *Austremerella*).

Ephemerellina, Demoulin, 1970:123. (Incl. *Lithogloea*).

Ephemerellina, McCafferty and de Moor, 1995:472. (Excl. *Lithogloea*).

Ephemerellina, Wang and McCafferty, 1995:193. (Revision).

DESCRIPTION OF MATURE LARVA

Head (Fig. 4) without well-developed marginal fringe of setae. Labrum (Fig. 13) broadly subquadrate, apical width approximately three times length, with scattered short setae over entire dorsal surface; apical margin broadly and gradually emarginate. Mandibles (Figs 22, 31) broadly robust; inner and outer incisors divergent; long mediolateral seta absent; outer incisor with at least one sharp denticle and apicomedial patch of setae developed on left mandible (Fig. 31). Maxillae as in Fig. 40. Superlinguae of hypopharynx extended distally beyond apices of lingua [Fig. 49, Fig. 12g of Demoulin (1970)], lateral margins nearly straight; lingua convex apically. Labium (Fig. 58) with well-demarcated glossae and paraglossae; paraglossae somewhat bluntly pointed medioapically. Prosternum (Fig. 65) with bi-lobular, spinous process medially. Forefemora (Fig. 4) relatively narrow. Tarsal claws (Fig. 70) with single row of denticles. Simple, filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-6; gills on abdominal segment 2 (Fig. 4) semi-operculate. Abdomen (Fig. 4) with single row of relatively narrow-elongate and sharp tubercles dorsally; posterolateral processes only poorly developed and approximate to base of following segment. Caudal filaments banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Forewings (Fig. 83) with IMP longer than MP₂ and both veins directly attached to each other in basal half of wing. Abdominal segments 2-6 (Fig. 89) with gill socket vestiges; abdominal terga 3-5 (sometimes others also) each with small, conical, medial tubercle vestige (Fig. 89). Median caudal filament well developed (three tailed).

DIAGNOSIS

The larvae of *Ephemerellina* are distinguished from those of other genera of Teloganodinae by their possession of a unique, spinous and bi-lobular, prosternal process, and by their possession of a labrum (Fig. 13) that is subquadrate, relatively broad, covered by short setae over nearly its entire dorsal surface, and somewhat emarginate along the apical margin. Larvae may be further distinguished from other African genera of Teloganodinae by their single row of relatively narrow-elongate dorsal abdominal tubercles. A combination of characteristics must be used to diagnose the adults of *Ephemerellina* from those of other Teloganodinae (see Key to Genera, above). They differ from other African genera of Teloganodinae by the presence of a single median row of conical tubercle vestiges on the abdominal terga.

SPECIES INCLUDED

Ephemerellina barnardi Lestage, 1924:348.
Ephemerellina sp. Allen and Edmunds, 1963a:15.

DISTRIBUTION

South Africa: Western Cape Province.

MATERIAL EXAMINED

Ephemerellina barnardi: SOUTH AFRICA: Male and female adults, Gt. Winterhoek Mts., 4500 ft., XI-1916, AM. Larva, Gt. Winterhoek Mts., IX, XI-1932, K. H. Barnard, AM. Larva, Cedarbergen, I-1930, K. H. Barnard, AM. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larva, Great Berg R., Lower forest reserve, Driefontein Bridge, VII-19-1950, AM. Larva, Viljoen's Pass, Elgin, S side, X-29-1931, K. H. Barnard, AM.

REMARKS

This monotypic genus is defined by the autapomorphic spinous, bi-lobular, prosternal process in the larvae (see also Phylogenetics, below). It can be viewed as the most plesiotypic genus of the Teloganodinae, in that it retains the greatest number of plesiomorphic character states. It also rivals *Austremerella* of the Austremerellinae as the most plesiotypic genus of the entire family. There have been various attempts to place representatives of other lineages in this genus. Allen (1965) considered *Austremerella* a subgenus of *Ephemerellina*. Demoulin (1970) considered *Lithogloea* a subgenus of *Ephemerellina*, and also placed species, either as subgenus *Ephemerellina* or subgenus unknown in *Ephemerellina* that actually belong to *Nadinella* **gen. nov.** From our cladistic analysis, it is now clear that symplesiomorphy was the basis of all of the above interpretations. Allen and Edmunds (1963a) and Tshernova (1972) placed certain species, now known to belong to *Vietnamella*, in the genus *Ephemerellina*. This latter situation was resolved by Wang and McCafferty (1995), and the historically confused taxonomy of African Teloganodidae is resolved herein. In Lestage's (1924) original description of the adults, he incorrectly reported two terminal segments of the male genital forceps. This was corrected by Barnard (1932), who at the same time, provided description of the larval stage.

Ephemerellina is known from temperate mountain streams in the extreme southwest of the African continent. We consider it a temperate Gondwanaland relict (see Biogeography discussion under Phylogenetics, below). The first author and N. McCafferty collected larvae in abundance from moss on vertical rock faces of waterfalls of small mountain tributaries of the Eerste River near Stellenbosch. Based on data from small tributaries and waterfalls, it appears that the habitat is similar to that of *Nadinella* **gen. nov.** (see below). King (1981) reported some spatial and temporal data for *E. barnardi* in the Eerste River. She found larvae throughout the year and most commonly from stones in the upper reaches of the river. Barber-James and de Moor (pers. comm.) indicated that larvae have been found on the straplike leaves (ca. 1 mm width) of *Isolepis* (Cyperaceae), where this plant occurs in mats in swift current of acidic streams of the Western Cape.

Genus *Nadinella* gen. nov.

(Figs 5, 14, 23, 32, 41, 50, 59, 66, 71, 74-76, 84, 90)

TYPE SPECIES

Ephemerellina crassi Allen and Edmunds.

DESCRIPTION OF MATURE LARVA

Head (Fig. 5) without well-developed marginal fringe of setae. Labrum (Fig. 14) subquadrate and relatively narrow, with apical width only approximately 1.5 times length; setae in transverse medial third of dorsum; apical margin deeply notched medially. Mandibles (Figs 23, 32) somewhat narrow in basal half and gradually broadening apically; incisors separated but not divergent; left mandible with outer incisor with three semi-blunt poorly demarcated denticles and without medioapical setal patch (Fig. 32). Maxillae as in Fig. 41. Superlinguae of hypopharynx (Fig. 50) moderately developed, rounded laterally, and subequal in length to lingua; lingua with apical margin nearly straight. Labium (Fig. 59) with well-divided glossae and paraglossae; glossae rounded apically; paraglossae bluntly pointed apically. Prosternum (Fig. 66) without medial spinous process. Forefemora (Fig. 5) relatively narrow. Tarsal claws (Fig. 71) with two rows of denticles. Simple, filamentous gills present or absent on abdominal segment 1; lamellate gills present on 2-5; gills on abdominal segment 2 (Fig. 5) semi-operculate. Abdomen (Fig. 5) with two rows of blunt dorsal tubercles, sometimes coalescing on some segments into short and broad, apically straight-margined or rounded processes (Figs 74-76); posterolateral processes poorly developed and approximate to base of following segment. Caudal filaments banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Forewings (Fig. 84) with IMP longer than MP₂, and both veins directly attached to each other in basal half of wing. Abdominal segment 2-5 with gill socket vestiges; abdominal terga 3-5 (sometimes others also) with small transverse thickening medially, each bearing two small, conical tubercle vestiges [see Figs 8c, 8d of Barnard (1940)]; tubercle vestiges may not be evident in some specimens. Male genitalia as shown in Fig. 89. Median caudal filament well developed (three tailed).

DIAGNOSIS

The larvae of *Nadinella* can be distinguished from larvae of all other genera of Teloganodinae by the presence of two rows of denticles on the claws, the relatively narrow and deeply notched labrum, and the double row of dorsal abdominal tubercles. Among the African genera of Teloganodidae, it can further be differentiated by the presence of lamellate gills on abdominal segments 2-5. *Ephemerellina* and *Lithogloea* larvae have lamellate gills on abdominal segments 2-6, and *Lestagella* larvae have lamellate gills on abdominal segments 2-4. Some *Nadinella* larvae have the double tubercles coalesced into a single, broad, posteromedian protuberance. *Lithogloea* larvae have single, somewhat broad, medial tubercles that may be blunt or sharp apically. In those *Nadinella* larvae in which the paired tubercles have become coalesced into a broad protuberance,

some bifurcation will usually still be evident on at least some of the segments. If no bifurcation is evident, then often some, if not most, of the protuberances will be very broad and straight along their apical margin [Figs 75, 76, Fig. 13l in Demoulin (1970)]. In any case, it would be prudent not to rely solely on the presence of the double row of tubercles for identifying *Nadinella*.

The adults of most *Nadinella* are distinct among the Teloganodinae, in that they have short, broad medial processes, with small paired tubercle vestiges evident on at least abdominal terga 3-5. They may be differentiated among the African genera of Teloganodidae by the presence of gill socket vestiges on abdominal segments 2-5. The former characteristic may not be evident on adults associated with those few larvae that have coalesced tubercles (see discussion, above), and the latter character can be difficult to see in some specimens. Because *Nadinella* has a relatively elongate IMP that is directly attached with MP₂, it cannot be confused with *Lithogloea* or *Lestagella*, even though the dorsal abdominal tubercle vestiges may not be evident in any of these genera. The male genitalia of *N. crassi* and *L. harrisoni* are also distinctive, particularly with regard to the shape of the penes (Figs 90, 91).

ETYMOLOGY

Nadinella is named for Nadine McCafferty, who was instrumental in carrying out the field work in South Africa that facilitated the study of Teloganodidae.

SPECIES INCLUDED

Nadinella brincki (Demoulin) **comb. nov.**

Ephemerellina brincki Demoulin, 1970:125.

Nadinella crassi (Allen and Edmunds) **comb. nov.**

Ephemerellina crassi Allen and Edmunds, 1963a:12.

DISTRIBUTION

South Africa: Western Cape Province.

MATERIAL EXAMINED

Nadinella crassi: SOUTH AFRICA: Holotype larva, paratype larvae and male subimago, Great Berg R., French Hoek Reserve, XI-20, 21-1950, A. D. Harrison, PERC. Larva, Gt. Winterhoek, IX,XI-1932, K. H. Barnard, PERC. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mts., waterfall of 1st trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek St. Forest, rivulet trib. Eerste R. IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mt. Reserve, Eerste R. near bridge at end of dirt road, IX-28-1990, W. P. and N. McCafferty, PERC. Subimago with larval exuviae, Great Berg R., railway bridge above Groot Drakenstein, XI-11-1953, AM.

Nadinella brincki: SOUTH AFRICA: Larva, Eerste Stellenbosch, X-25-1930, AM (incorrectly labeled by K. H. Barnard as *Lithogloea harrisoni*).

Nadinella sp.: SOUTH AFRICA: Krugersdorp R., III-8-1960, AM.

REMARKS

This genus is defined by the autapomorphic double row of denticles on the tarsal claws (see also Phylogenetics, below). The deeply notched condition of the labrum also appears to be autapomorphic within the Teloganodidae, but we do not know how consistent it will prove to be on a generic level. Demoulin (1970) originally considered *N. crassi* as “*Ephemerellina* (subg.?).” He also described at that time what he termed as the “simplex” form of *N. brincki* and placed it in *Ephemerellina* (subgenus *Ephemerellina*). This latter species, however, clearly belongs to *Nadinella*, having the double row of claw denticles, lamellate gills on abdominal segments 2-5, etc. It is atypical of most of the individuals we have seen of *Nadinella*, in that the usual double row of dorsal abdominal tubercles has coalesced into a single broad and straight-margined tubercle, or protuberance. We do not know if this represents a variation of *N. brincki* or perhaps another species. Presumably, it lacks the simple gills on abdominal segment 1, although this is not clear from Demoulin’s account. We have seen variations of *N. crassi* (a species with simple gills on abdominal segment 1) with similar, and even more extreme, tubercle variation (Figs 74-76). Barnard (1940) included an adult of *Nadinella* as part of a series of *Ephemerellina barnardi* Lestage. The presence of a double row of tubercle vestiges on the terga of that specimen [Figs 8c, 8d of Barnard (1940)] clearly excludes it from *Ephemerellina*.

Nadinella is restricted to temperate mountain streams in the extreme southwest of the African continent. We consider it a temperate Gondwanaland relict (see Biogeography discussion under Phylogenetics, below). The first author collected larvae in abundance from moss growing on the rock faces of waterfalls of tributaries of the Eerste River near Stellenbosch, as well as from habitats with less gradient. We have also seen collecting labels for *Nadinella* larvae that specifically noted that they had been taken in *Wardia* moss on rocks.

Genus *Lithogloea* Barnard

(Figs 6, 15, 24, 33, 42, 51, 60, 67, 72, 85, 91)

Lithogloea Barnard, 1932:252. (Larva and adult). Type: *Lithogloea harrisoni* Barnard, by monotypy.

Ephemerellina (subgenus *Lithogloea*), Demoulin, 1970:128.

Lithogloea, McCafferty and de Moor, 1995:472.

DESCRIPTION OF MATURE LARVA

Head (Fig. 6) without well-developed marginal fringe of setae. Labrum (Fig. 15) with apical margin nearly straight and lateral margins slightly convergent apically; dorsal surface with irregular transverse rows of setae at midlength and apical fourth; basal width approximately twice length. Mandibles (Figs 24, 33) narrowed, slightly broader apically; inner and outer incisors divergent; long mediolateral seta absent; left mandible with outer incisor with at least one sharp denticle and without apicomedial patch of setae (Fig. 33). Maxillae as in Fig. 42. Superlinguae of hypopharynx (Fig. 51) with apical margins approximately subequal with that of lingua, lateral margins rounded; lingua convex apically. Labium (Fig. 60) with well-divided glossae and paraglossae; paraglossae somewhat bluntly pointed medioapically. Prosternum (Fig. 67) without bi-lobular, spinous process. Forefemora (Fig. 6) relatively narrow. Tarsal claws with single row of denticles. Simple filamentous gills present on abdominal segment 1; lamellate gills on abdominal segments 2-6; gills on abdominal segment 2

(Fig. 6) semi-operculate. Abdomen (Fig. 6) with single row of poorly developed, short, usually broad-based tubercles dorsally; posterolateral processes well developed, elongate-subtriangular, sharply attenuated, and well separated from base of following segment; middle segments with short lateral setae (Fig. 6). Caudal filaments banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Forewings (Fig. 85) with IMP shorter than MP_2 and detached from it. Abdominal segments 2-6 with gill socket vestiges; abdominal terga without tubercle vestiges. Male genitalia as shown in Fig. 91. Median caudal filament well developed (three tailed).

DIAGNOSIS

The larvae of *Lithogloea* are distinguished from those of other genera of the Teloganodinae by their well-developed, elongate, and remote abdominal posterolateral processes, which are widely separated from the base of the following segment. At least one species of the Oriental genus *Teloganodes* also has posterolateral processes nearly as developed as those of the *Lithogloea*, and *Lestagella* has moderately developed posterolateral processes. In the latter genera, however, gills are absent on abdominal segment 6, there is a well-developed setal fringe on the head, and lateral abdominal setae are much longer. With respect to dorsal abdominal tubercles, there are some aberrant forms of *Nadinella* that could be confused with *Lithogloea*. This situation is discussed in the Diagnosis of *Nadinella*, above. Adults of *Lithogloea* are distinguished from those of other genera of Teloganodinae by the combination of an IMP in the forewings that is much shorter than MP_2 and detached from it, and the presence of gill socket vestiges on abdominal segments 2-6. The nearly apically truncate penes (Fig. 91) of *Lithogloea* should also be of some aid in differentiating the adult in Africa.

SPECIES INCLUDED

Lithogloea harrisoni Barnard, 1932:253.

Ephemerellina harrisoni (Barnard), Demoulin, 1970:129.

Lithogloea harrisoni Barnard, McCafferty and de Moor, 1995:472.

DISTRIBUTION

South Africa: Western Cape. There are unconfirmed records of *Lithogloea* from the Eastern Cape Prov. and Kwazulu-Natal Prov., South Africa (Crass 1947), Swaziland (Stander 1963), and the Northern Transvaal Prov., South Africa and Malawi (Harrison and Agnew 1962). We have seen material labeled *Lithogloea* spp. in the Albany Museum from the Crocodile River (Eastern Transvaal), Schageni, Karino, the Itawa River (Zambia), Usutu River (Swaziland), and Malawi all collected in the 1950's and 60's. These all represent misidentified material of *Ephemerythus* Gillies (Tricorythidae). *Ephemerythus* was not described until 1960 (Gillies 1960), and up to that time had been known as "ephemerellid genus ?" (e.g., Kimmins 1955). It remains poorly known by non-specialists. A record of *Lithogloea* from Zaire by Marlier (1954) is most likely attributable to the baetid genus *Acanthiops* Waltz and McCafferty (see Barber-James and McCafferty 1997). Whereas it is possible that *Lithogloea* eventually may be confirmed from temperate and mountainous areas of the Eastern Cape and Kwazulu-Natal provinces of South Africa, we have been unable to substantiate

such a distribution at this time, and a more northern range in Africa can neither be substantiated nor is it predicted by the general biogeography of Teloganodidae (see Biogeography under Phylogenetics, below). In fact, the only materials of actual teloganodines that we have examined from outside the Western Cape are *Lestagella* from the Eastern Cape, misidentified and mislabeled as *Lithogloea*, and all of what Crass referred to as *Lithogloea* may be attributable to *Lestagella*. This is understandable because *Lestagella* was not known until 1970 (Demoulin 1970) and was not generally recognized after that. From all of the above we must assume that *Lithogloea* is restricted to the Western Cape of South Africa.

MATERIAL EXAMINED

Lithogloea harrisoni: SOUTH AFRICA: Male and female adults, Gt. Winterhoek, XI-1932, K. H. Barnard, AM. Subimagos, Gt. Drakenstein. Larva, West Cape, Jonkershoek Mts., Eerste R. nr bridge at end of dirt rd, IX-28-1990, W. P. and N. McCafferty, PERC.

REMARKS

This genus is defined by the autapomorphic well-developed, elongate abdominal posterolateral processes (see also Phylogenetics, below). The bluntly fused and pointed maxillae that lack denticles also appear to be unique within the family; the maxillae of *Lestagella* are also reduced, but differently. Barnard (1932) originally described *Lithogloea* based on *L. harrisoni*. Later he (Barnard 1940) recognized part of the material he had considered as *L. harrisoni* as another species *L. penicillata*, which was later recognized as another genus, *Lestagella*, by Demoulin (1970).

Little is known of the ecology of this species. It was not taken from waterfalls in the Jonkershoek Mountains by the first author as was *Nadinella* and *Ephemerellina*, but was found cohabiting with them in other habitats with less gradient. King (1981) and King et al. (1988) provided some spatial and temporal data with respect to *L. harrisoni* in the Jonkershoek mountain reaches of the Eerste and Long rivers. Larvae have recently been taken on the 1 mm wide leaves of *Isolepis* (Cyperaceae), where this plant occurs in mats in swift currents of certain streams in the Western Cape (Barber-James and de Moor, pers. comm.). The range of *Lithogloea* is somewhat dubious at this time (see Distribution, above), and records other than those from the Western Cape need to be authenticated with further study of material. Such records are likely attributable to *Lestagella*, because that genus was not recognized as a separate genus until after the questionable records appeared. Since workers were presumably using Barnard (1940) for identification, they would have easily confused *Lithogloea* and *Lestagella*.

Genus *Lestagella* Demoulin

(Figs 7, 16, 25, 34, 43, 52, 61, 68, 72, 86)

Lestagella Demoulin, 1970:130. (Larva and adult). Type: *Lithogloea penicillata* Barnard, by original designation.

DESCRIPTION OF MATURE LARVA

Head (Fig. 7) with well-developed marginal fringe of setae, long anteriorly, shorter laterally. Labrum (Fig. 16) with rounded lateral margins and slightly emarginate apical margin; dorsum with

medial transverse row of setae; basal width nearly three times length. Mandibles (Figs 25, 34) narrow throughout and atrophied apically; mediolateral elongate seta present, not bristlelike, sometimes broken or missing; left mandible without apicomedial setal patch (Fig. 34). Maxillae as in Fig. 43. Superlinguae of hypopharynx (Fig. 52) shorter than lingua, with straight lateral margins; apical margin of lingua with small notch medially. Labium (Fig. 61) with poorly divided glossae and paraglossae; paraglossae rounded apically. Prosternum (Fig. 68) without bi-lobular, spinous process medially. Forefemora (Fig. 7) broad. Tarsal claws (Fig. 73) with single row of denticles. Simple filamentous gills present on abdominal segment 1; lamellate gills present on abdominal segments 2-4; gill on abdominal segment 2 (Fig. 7) fully operculate. Abdomen (Fig. 7) without dorsal abdominal tubercles; posterolateral processes subtriangular and moderately developed, not elongate and sharply attenuated, and moderately separated from base of following segment; middle segments with long lateral setae (Fig. 7). Caudal filaments banded; median caudal filament well developed (three tailed).

DESCRIPTION OF ADULT

Forewings (Fig. 86) with IMP shorter than MP_2 and detached from it. Abdominal segments 2-4 with gill socket vestiges; abdominal terga without dorsal abdominal tubercle vestiges. Median caudal filament well developed (three tailed).

DIAGNOSIS

Lestagella larvae can be told from larvae of other Teloganodinae by the reduced and atrophied mandibles, the modified apices of the maxillae, and the medial notch of the lingua of the hypopharynx. Other than these mouthpart characteristics, which will require slide mounting to examine efficiently and may possibly prove to be species specific, the combination of the three tails and the well-developed marginal fringe of setae on the head will distinguish the larvae of *Lestagella* from all others. The adults of *Lestagella* can be told from those of all other teloganodines by the combination of three tails, the relatively short and detached IMP in the forewings, and the presence of gill socket vestiges only on abdominal segments 2-4.

SPECIES INCLUDED

Lestagella penicillata (Barnard).

Lithogloea penicillata Barnard, 1940:637.

DISTRIBUTION

South Africa: Western Cape and Eastern Cape. Unusual specimens from the Amatola Mountains of the Eastern Cape were tentatively identified as *Lithogloea harrisoni* by Crass (1947). Although we could not find that material, we maintain that the record is attributable to either *Lestagella* or *Ephemerythus* (family Tricorythidae). Other materials we have seen labeled as *Lithogloea* are actually *Lestagella*. The latter two genera have been commonly misidentified as *Lithogloea* (see Distribution, under *Lestagella*).

MATERIAL EXAMINED

Lestagella penicillata: SOUTH AFRICA: Larvae, South Cape, Wit R., IX-18-1989, AM. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larva, West Cape, Jonkershoek Mts., waterfall of 1st trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mts. Reserve, Eerste R., nr bridge at end of dirt rd, IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, upper Kirstenbosch Nat'l. Bot. Gard., Skeleton Gorge Stream, X-1-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Kirstenbosch Nat'l. Bot. Gard., Window Stream at rd, IX-29-1990, W. P. and N. McCafferty, PERC. Larva, Eastern Cape, Madonna and Child, X-7-1989, AM. Subimago and larvae, Tweck's Pont, IX-1933, K. H. Barnard, AM. Larvae, Gt. Winterhoek Mts., IX-11-1932, K. H. Barnard, AM.

REMARKS

This genus is defined by the autapomorphic atrophy of the apical mandibular armature (see also Phylogenetics, below). The notched lingua of the hypopharynx also appears unique among the Teloganodidae. *Lestagella* belongs to a clade that also includes the Oriental genera *Macafertiella* and *Teloganodes*. As such, it represents a transition between the archaic African fauna and the Oriental teloganodines (see Biogeography under Phylogenetics, below). Barnard (1940) originally considered this genus as part of *Lithogloea*; however, Demoulin (1970) recognized its distinctiveness and established the genus.

Although *Lestagella* is known from a number of mountain streams in the Western and Eastern Cape, little is known of its ecology.

Genus *Macafertiella* Wang

(Figs 8, 17, 26, 35, 44, 53, 62)

Macafertiella Wang (in Wang and McCafferty), 1996:15. (Larva). Type: *Macafertiella insignis* Wang and McCafferty, by original designation.

DESCRIPTION OF MATURE LARVA

Head (Fig. 8) with well-developed marginal fringe of setae, setae longest posterior to antennae. Labrum (Fig. 17) with distally convergent lateral margins and slightly emarginate apical margin; dense transverse row of long filtering setae located at approximately 3/4 distance from base and curved laterally, following marginal shape of labrum; basal width approximately three times length. Mandibles (Figs 26, 35) narrow throughout, slightly broader apically; long mediolateral seta present, bristlelike; left mandible with outer incisors blunt and not divergent, and with sparse medioapical patch of setae (Fig. 35). Maxillae as Fig. 44. Superlinguae of hypopharynx (Fig. 53) extending beyond lingua, with straight lateral margins; apical margin of lingua straight with slightly produced area medially. Labium (Fig. 62) with poorly divided glossae and paraglossae; glossae nearly completely fused medially; paraglossae rounded apically. Prosternum without bi-lobular, spinous process medially. Forefemora (Fig. 8) relatively narrow. Tarsal claws with single row of denticles. Simple filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-6; gill on abdominal segment 2 (Fig. 8) fully operculate. Abdomen (Fig. 8) with single row of sharp medial tubercles dorsally; posterolateral processes poorly developed and approximate

to base of following segment. Cerci not banded. Median caudal filament vestigial (two tailed).

ADULT UNKNOWN

DIAGNOSIS

Larvae of *Macafertiella* are distinguished from those of other Teloganodinae by the unique labrum, but also by the combination of being two tailed and having gills on abdominal segment 6. Although initially Wang and McCafferty (1996b) indicated there were size differences between the abdominal tubercles of *Macafertiella* and *Teloganodes*, the range in size of *Teloganodes* tubercles has since been found to include the size of those of *Macafertiella*. The adults are unknown, but assuredly will have a reduced median caudal filament as well as larva-associated vestiges of the median row of dorsal abdominal tubercles and gill socket vestiges on abdominal segment 2-6. Together, these should allow recognition of the unknown adult and prevent confusion with the genus *Teloganodes*, which may be taken sympatrically and is similarly two tailed, but which has no gill socket vestiges on abdominal segment 6.

SPECIES INCLUDED

Macafertiella insignis Wang and McCafferty, 1996:16.

DISTRIBUTION

Sri Lanka.

MATERIAL EXAMINED

Macafertiella insignis: SRI LANKA: Larval holotype and paratype, Belihuloya Region, Veli-Oya, trib. of Walawe-Ganga, 700 m, XII-8-1970, F. Starmühlner, PERC. Larva paratype, Kitilgala Region, Rambukpoth-Oya, nr Pitawela, trib. Kelani-Ganga, 650 m, XII-27-1970, F. Starmühlner, PERC.

REMARKS

This genus is defined by the apomorphic labrum and labral setation (see also Phylogenetics, below). Although *Macafertiella* is clearly a sister group of *Teloganodes* and a member of a rather distinctive clade consisting also of *Lestagella*, it is somewhat aberrant, particularly with respect to mouthparts and legs. It has been found cohabiting with undescribed species of *Teloganodes* as well as *T. tristis* in Sri Lanka. There remains the possibility that the larvae of *M. insignis* is associated with an adult from Sri Lanka that was named *Teloganodes major* by Eaton (1884). If this proves to be true, then *T. major* would become the type of *Macafertiella*. Virtually nothing is known of the ecology of *Macafertiella*.

Genus *Teloganodes* Eaton

(Figs 9, 10, 18, 19, 27, 28, 36, 37, 45, 46, 54, 55, 63, 64, 87)

Teloganodes Eaton, 1882:208. (Adult). Type: *Cloe tristis* Hagen, by original designation.
Teloganodes, Ulmer, 1939:627. (Larva).

DESCRIPTION OF MATURE LARVA

Head (Figs 9, 10) with well-developed marginal fringe of setae, longer setae posterior to antennae (Fig. 9) or over entire margin (Fig. 10). Labrum (Figs 18, 19) with tapering lateral margins, and slightly emarginate apical margin; dorsum with transverse area of setae at midlength area or slightly beyond midlength; basal width approximately 2.5 times length. Mandibles (Figs 27, 28, 36, 37) narrow; long mediolateral seta present and bristlelike; left mandible with incisors separate and juxtaposed with denticles of outer incisor blunt (Fig. 36), or with denticles of outer incisor fused and blunt (Fig. 37). Maxillae (Figs 45, 46) often with small lateral nodules. Superlinguae of hypopharynx (Figs 54, 55) shorter than lingua, with lateral margins slightly concave; apical margin of lingua convex. Labium (Figs 63, 64) with glossae and paraglossae very poorly divided, glossae nearly completely fused medially; paraglossae rounded apically. Prosternum without bi-lobular, spinous process medially. Forefemora (Figs 9, 10) relatively broad. Tarsal claws with single row of denticles. Simple, filamentous gills on abdominal segment 1 absent; lamellate gills present on abdominal segments 2-4 or 2-5; gills on abdominal segment 2 (Figs 9, 10) fully operculate. Abdomen with single row of poorly to well-developed dorsal tubercles (Fig. 9) or without dorsal tubercles (Fig. 10); posterolateral processes poorly (Fig. 9) to moderately developed (Fig. 10), if moderately developed, then posterolateral processes slightly upturned and middle segments with long lateral setae (Fig. 10). Cerci not banded. Median caudal filament reduced (two tailed).

DESCRIPTION OF ADULT

Forewings (Fig. 87) with IMP shorter than MP₂ and detached from it. Abdominal segments 2-4 or 2-5 with gill socket vestiges; abdominal terga with or without median row of tubercle vestiges. Median caudal filament reduced.

DIAGNOSIS

The larvae of *Teloganodes* are distinguished from those of other Teloganodinae by the combination of being two tailed and having no gills on abdominal segment 6. The adults of Teloganodinae can be told from those of other Teloganodinae by the combination of the two-tailed condition and the absence of gill socket vestiges on abdominal segment 6.

SPECIES INCLUDED

- Teloganodes dentata* Navás, 1931:19.
- Teloganodes lugens* Navás, 1933:17.
- Teloganodes major* Eaton, 1884:136.
- Teloganodes tristis* (Hagen).
- Cloe tristis* Hagen, 1858:476.
- Teloganodes tristis* (Hagen), Eaton, 1884:135.

DISTRIBUTION

Southern Asia: China: Zhejiang Province (Navás 1933); Hong Kong (Dudgeon 1990); India: Maharashtra Province (Navás 1931); Indonesia: Borneo, Celebes, Java (Ulmer 1939), Lombok, Sumatra (Ulmer 1939); Malaysia: Sabah, West Malaysia; Philippines; Sri Lanka.

MATERIAL EXAMINED

(All material deposited in PERC; all material larvae, except where noted).

Teloganodes tristis: MALAYSIA (EAST): Sabah, Sungai Moyog, 3 mi E of Penampang, IX-27-29-1978, G. F. and C. Edmunds. Sabah, Sungai Moyog at trib. 8 mi E Penampang, X-1-1978, G. F. and C. Edmunds. MALAYSIA (WEST): Larvae and male subimagos, Selangor, large trib. Sungai Selangor, 6 mi NE Kota Kuba Baharu (Mile 44), XI-1-1987, G. F. and C. Edmunds. SRI LANKA: Male adults and larva, Ceylon, Newara Eliya Dist., Bakers Falls nr Farr's Inn, Horton Plains, 7000', VIII-28-1968.

Teloganodes spp: INDONESIA (BORNEO): Kalimantan Timur Prov., Waterfall and stream, 11 km NE of Samarinda, VIII-27-1985, J. T. and D. A. Polhemus. INDONESIA (CELEBES): Sulawesi Selatan Prov., Pattunuang R., 7 km SW of Bantimurung, X-13-1985, 0-100 m, J. T. and D. A. Polhemus. Sulawesi Tengah Prov., stream 10 km SE Kamarora, Lore Lindu Nat. Park, 830 m, X-8-1985, J. T. and D. A. Polhemus. Sulawesi Utara Prov., Toraut R., Dumoga-Bone Nat. Park 0°34'N, 123°53-54'E, IX-3-5-1985, D. A. Polhemus. Sulawesi Utara Prov., upper Metelanga R., 10 km S. of Doloduo, IX-4-7-1985, J. T. and D. A. Polhemus. Sulawesi Utara Prov., forest stream S. of Lake Mala, 1200 m, IX-11-1985, D. A. Polhemus. INDONESIA (LOMBOK): Nusa Tenggara Barat Prov., Aik Jut R., 1 km N of Sesaot, 30 km NE Mataram, X-23-1985, 350 m, J. T. and D. A. Polhemus. MALAYSIA (EAST): Sabah, Sungai Moyog at tributary 8 mi E of Penampang, X-1-1987, G. F. and C. Edmunds. Sabah, Sungai Moyog, 3 mi E of Penampang, IX-27-29-1987, G. F. and C. Edmunds. Sabah, Sungai Tuaran, Tamparuli, X-3-1987, G. F. and C. Edmunds. Sabah, Liwagu, Moyog, N of Kundassan, 915 m, VIII-16-17-1972, G. F. and C. Edmunds. Sabah, Liwagu R. at bridge, Ranau, 335 m, VIII-11-16-1972, G. F. and C. Edmunds. Pahang, Fraser Hill, Jeriau Falls (20°C), VIII-30-1978, G. F. and C. Edmunds. MALAYSIA (WEST): Perak, Sungai Jor: Cameron Highlands Road, 19 Prov., IX-22-23-1978, G. F. and C. H. Edmunds. Larvae, male and female subimagos, Selangor, large trib. Sungai Selangor, 5 - 10 mi. NE Kota Kuba Baharu (Mile 42, 43, 44, 48), 31-VIII-78, IX-1-13-1978, G. F. and C. Edmunds (24°C). Selangor, Sungai Tua, 2 - 6 mi. N. Batu Caves, IX-14-15-1978, G. F. and C. Edmunds. Selangor, trib. of Sungai Gombak, 16 mi., 27-VIII-78, G. F. and C. Edmunds. Selangor, Sungai Kanching, Templer Park, VIII-28-1978, G. F. and C. Edmunds. Trengganu, Kampong Sungai Tong, IX-9-1978, G. F. and C. Edmunds. PHILIPPINES: Leyte, Leyte Prov., Lusig R. at Hilusig, VII-15-1985, J. T. and D. A. Polhemus. Leyte, Leyte Prov., Pangusungan R., N. of Baybay, CL 1988, VII-17-1985, J. T. and D. A. Polhemus. Luzon, Benguet Prov., 7 km, Asia Hot Springs Rd., VII-7-1985, J. T. and D. A. Polhemus. Luzon, Benguet Prov., stream below Camp John, Hay hydro. nr. Tuba mines, VII-8-1985, 900 m, J. T. and D. A. Polhemus. Luzon, Pangasinan Prov., Bayaling R., 100 m, 15 km E. of Bauang, VII-6-1985, J. T. and D. A. Polhemus. Luzon, Quezon Prov. Nat. Botanic Gardens, Llavac, VII-11-1985, J. T. and D. A. Polhemus. Mindanao, South Cotabato Prov., Lahit R., nr. Lake Sebu, VII-19-1985, J. T. and D. A. Polhemus. Mindanao, Zamboanga del Sur Prov., Bituti R., 7 km NW of Zamboanga City, 100 m, VII-22-1985, J. T. and D. A. Polhemus. Larva, female adult, Mindoro, Mindoro Oriental Prov., Apararai Cr., 22 km SW of Calapan, VII-13-1985, J. T. and D. A. Polhemus. SRI LANKA: Deniyaya Region, Meda-dola trib. of Gin-Ganga R., Sinharaja Range 1000 m, XI-9-1971, F. Starmühlner. Deniyaya Region, Nagahaketa-Dola trib. of Nilwala-Ganga R. 500 m, XI-13-1970, F. Starmühlner. Deniyaya Region, Campden Hill Dola trib. of Gin-Gana R., 700 m, XI-9-1970, F. Starmühlner. Deniyaya Region, Nagahaketa-Dola trib. of Nilwala-Ganga R., 500 m, XI-13-1970, F. Starmühlner. Deniyaya Region, Campden Hill Dola trib. of Gin-gana R., 700 m, XI-11-1970, F. Starmühlner. Kitulgala Region,

Ambukpoth-Oya, near Pitawela, trib. of Kelani-Ganga, 650 m, XII-26-27-1970, F. Starmühlner. Kitulgala Region, Kelani Ganga near resthouse by Kitulgala, XII-28-1970, F. Starmühlner. Kitulgala Region, Hal-Oya near Ginigathhena, trib. of Kelani-Ganga 700 m, XII-27-1970, F. Starmühlner. Maskeliya Region, Gartmore Dola 2000 m, at waterfall XI-29-1970, F. Starmühlner. Maskeliya Region, backwaters of Gartmore Dola waterfall, 1800 m, XI-30-1970, F. Starmühlner. Maskeliya Region, Mocha R., trib. of Maskeliya R., dam by Adam's Peak estate, 1800 m, XI-28-1970, F. Starmühlner, PERC. Maskeliya Region, Maskeliya R. at base of Adam's Peak, about 1 km above Maskeliya impoundment 1800 m, XII-7-1970, F. Starmühlner. Maskeliya Region, Hakgala-Dola brook above Hakgala, near Nuwara Eliya 2000 m, XII-2-1970, F. Starmühlner. Ratnapura Region, Ira-Handha-Pana-Ela, right bank fork trib. of Kalu-Ganga R., 100 m, XI-23-1970, F. Starmühlner.

REMARKS

This genus is defined by the loss of gills on abdominal segment 6 within the *Macafertiella* + *Teloganodes* lineage (see also Phylogenetics, below). It is a relatively diverse and highly apotypic genus, showing some variability in characters that are stable in other genera of Teloganodidae. Eaton (1882) named the genus for Sri Lankan adults that had previously been described under the genus *Cloe* by Hagen (1858). Eaton (1884) added an additional species from Sri Lanka, *T. major*, also known only from the adult, and figured a forewing of an unnamed species from West Malaysia. We can assume that Eaton's generic placement of these additional species was correct, since he was aware of the fact that *Teloganodes* lacks a middle tail. Nonetheless, his *T. major* could eventually prove to be the adult of *Macafertiella*, which is also known from Sri Lanka. Ulmer (1924) provided the first male adult description. Navás (1931) described a species from India, *T. dentata*, and one from China, *T. lugens*, both based only on adults. Ulmer (1940) described the larval stage of *Teloganodes* for the first time as *T. tristis*, from Sumatra and Java. We have examined larvae from Sri Lanka that are almost identical to those described by Ulmer, and therefore consider his species identification correct. Hubbard and Pescador (1978) reported *T. tristis* from the Philippines.

Very little is known of the ecology of the genus *Teloganodes*. Hubbard and Peters (1984), however, indicated that, in Sri Lanka, larvae were taken from 90-2100 m, always on stones in swift currents in small to large streams (sometimes at waterfalls), with water temperatures ranging from 14°C to about 26°C. Our records also show that *Teloganodes* is common in waterfalls, also having been taken from waterfalls in Borneo by J. T. and D. A. Polhemus and from waterfalls in Sri Lanka by F. Starmühlner (see Material examined, above). These data are in general agreement with data available on the African Teloganodinae, resulting from collections by the first author and N. McCafferty of *Ephemerellina* and *Nadinella* in abundance at waterfalls.

PHYLOGENETICS

CLADISTICS

Cladistic methodology for deducing phylogeny is after Ross (1937, 1974) and Hennig (1950, 1966). Operational taxonomic units (OTUs) analyzed consisted of eight distinctive species groups (Fig. 1) that each appeared monophyletic, based on their possession of unique or specialized characteristics (cladistic analysis substantiated monophyly for each OTU). The outgroup for determining character state polarity consisted of all other pannote mayflies.

Thirty comparative characters with different character states distributed among the OTUs were used in the analysis, and these are presented in terms of their apomorphic and plesiomorphic states in Table 2. Among the cladistic characters, 20 have only one apomorphy expressed in the

Teloganodinae; three are phenoclinal within the Teloganodidae in that there are two stepwise apomorphies, the first of which is transitional to the next (see apomorphies 12 and 24; 21 and 26; 22 and 27); and two are bi-directional, in that the two apomorphies cited are different and independent (see apomorphies 6 and 23; 8 and 17).

Results of the cladistic analysis are given in the form of a most parsimonious cladogram (Fig. 1) deduced from our data. Numbers in Figure 1 refer to all synapomorphies that define the particular clade or lineage where they appear and correspond to those listed in Table 2. Some of these character states are given in abbreviated form in the table, but details can be found in the text and figures.

CHARACTER EVOLUTION

The deduced cladogram (Fig. 1) represents the most parsimonious arrangement that could be generated from our data; it is not, however, the only alternative. Thus, in accepting the parsimonious cladogram, convergences with respect to some character states must also be accepted. Below, we present an interpretation of character state evolution, particularly in regard to homoplasy, that must be accounted for in light of the deduced phylogeny of the Teloganodidae.

Multistate phenoclinal characters are often highly indicative of phylogenetic relationships (Ross 1974). We interpret that this is also the case in the Teloganodidae. One phenocline involves the relative operculate nature of the gills on abdominal segment 2 [see apomorphies 12 and 24 (Fig. 1, Table 2)], in which the semi-operculate condition (12) is intermediate to the full operculate condition (24). A parallel transition is seen in the phylogeny of the *Timpanoga* complex (Ephemerellidae) (McCafferty and Wang 1994). The second phenocline involves the development of the long mediolateral seta on the mandibles [see apomorphies 21 and 26 (Fig. 1, Table 2)], in which the appearance of a long hairlike seta (21) is intermediate to that seta becoming bristlelike (26). Such a bristlelike seta has been independently derived in the Prosopistomatidae. The third phenocline involves the degree of fusion of the glossae [see apomorphies 22 and 27 (Fig. 1, Table 2)], in which the poorly divided condition (22) is intermediate to the nearly completely fused condition (27). Numerous other synapomorphies express the same branching sequence as demonstrated by these phenoclines.

Lestagella, *Nadinella*, *Ephemerellina*, and *Lithogloea* all possess distinctive black bands on the larval caudal filaments, and this characteristic might very likely represent an apomorphy. Nonetheless, the most apotypic members (*Macafertiella* and *Teloganodes*) of the clade that also includes these four (Fig. 1) do not have the black banding. Because of the distinctive synapomorphies that define the entire large clade [apomorphies 11-12 (Fig. 1, Table 2), we hypothesize that the black banding was secondarily lost in the ancestor of *Macafertiella* and *Teloganodes*, both of which also lost the developed middle tail. The appearance of the black banding in various members of the family Ephemerellidae and Neoephemeridae, for example, indicates that this is probably an adaptive characteristic.

From the parsimonious cladogram (Fig. 1), it appears that the loss of certain gill pairs occurs independently, and therefore must either not be used, or used with caution, for deducing phylogeny. In the case of the Teloganodidae larvae, the loss of the already reduced gills on abdominal segment 1 is one example of not being usable. The loss of this gill pair evidently has occurred independently in three different lineages: *Austremerella*, *Ephemerellina*, one species of *Nadinella*, and in the *Macafertiella* + *Teloganodes* lineage. Although the absence of these simple filamentous gills may help distinguish individual lineages, the character must be discounted for phylogenetic deduction,

TABLE 2. Character states used to hypothesize phylogenetic relationships of the higher taxa of Teloganodidae [numbered apomorphies are cited on the cladogram (Fig. 1)]

Apomorphy	Plesiomorphy
1. Male forceps segment 1 elongate (Figs 90, 91).	1'. Forceps segment 1 short.
2. Forewing stigmatic area subdivided into rows of cellules (Figs 80-82).	2'. Stigmatic area not modified as such (Figs 83-87).
3. Cerci medially with long and dense setae (Figs 77, 78).	3'. Cerci without such long and dense setae (Fig. 79).
4. Cephalic horns present (Fig. 3).	4'. Cephalic horns absent.
5. Mandibular incisors laterally oriented (Figs 21, 30).	5'. Incisors distally oriented (e.g., Figs 20, 29).
6. Paraglossae apically truncate (Fig. 57).† [see 23]	6'. Paraglossae somewhat pointed (e.g., Figs 56, 58).
7. Forewings with most short intercalaries attached basally (Figs 81, 82).	7'. Most marginal intercalaries free (e.g., Figs 80, 83).
8. Larval claws with single basal denticle. (Fig. 69).† [see 17]	8'. Claws with single row of denticles (Figs 70, 72, 73).
9. Labial palpal segment 3 elongated (Fig. 56).	9'. Segment short (e.g., Figs 77, 78).
10. Adult mesothorax with posterior processes (Fig. 88).	10'. Mesothorax not modified.
11. Gills on abdominal segment 7 absent.	11'. Gills 7 present.
12. Gills on abdominal segment 2 covering large portion of following gills (Figs 4-10).* [see 24]	12'. Gills 2 not covering more than half of following gill (Figs 2, 3)
13. Larval prosternum with spinous bi-lobular process (Fig. 65).	13'. Prosternum without process (Figs 66-68).
14. Labrum with dorsal setae in medial rows (Figs 14-19)	14'. Labrum with scattered setae dorsally (Figs 11, 13).
15. Mandibles narrowed (Figs 23-28).	15'. Mandibles robust (Figs 20, 22).
16. Left mandibles with medioapical setal patch reduced (Figs 32-36).	16'. Left medioapical setal patch developed (Figs 29-31).
17. Larval claws with two rows of denticles (Fig. 71).† [see 8]	17'. Claws with one row of denticles (Figs 70, 72-73).
18. Forewings with IMP shorter than, and detached from, MP ₂ (Figs 85-87).	18'. IMP long and directly attached with MP ₂ (Figs 80-84).
19. Larval abdominal posterolateral processes elongate-triangular and widely separated from base of following segment (Fig. 6)	19'. Posterolateral processes moderately developed and approximate (Figs 2, 3, 4, 5, 8, 9).
20. Larval cephalic setal fringe well developed, at least anterior to eyes (Figs 7-10).	20'. Setal fringe not developed (Figs 2, 4-6).
21. Mandibles with elongate mediolateral seta (Figs 34-37).* [see 26]	21'. Mandibles without such seta (Figs 29-33).
22. Glossae and paraglossae poorly divided (Figs 61-64).* [see 27]	22'. Glossae and paraglossae deep divided (Figs 56-60).
23. Paraglossae rounded apically (Figs 61-64).† [see 6]	23'. Paraglossae somewhat pointed (Figs 56, 58-60).
24. Gills on abdominal segment 2 fully operculate (Figs 7-10).* [see 12]	24'. Gills 2 semi-operculate (Figs 4-6).
25. Incisors and molae of mandibles atrophied (Figs 25, 34).	25'. Incisors and molae not reduced.
26. Mandible with long mediolateral seta well developed and bristlelike (Figs 35-37).* [see 21]	26'. Seta not bristlelike (Fig. 34).
27. Glossae nearly fused (Figs 62-64).* [see 22]	27'. Glossae poorly divided (Fig. 61).
28. Median caudal filament reduced in both adults and larvae (Figs 8-10).	28'. Three tailed (Figs 2-7).
29. Labrum with dense, curved row of long filtering setae dorsally (Fig. 17).	29'. Setae not as developed (Figs 14-16, 18, 19).
30. Gills 6 absent.	30'. Gills 6 present.

* One of two phenoclinical apomorphies of the character.

† One of two bi-directional apomorphies of the character.

because only in the case of the common ancestry of *Macafertiella* and *Teloganodes* would it have served as a supplementary defining synapomorphy. The loss of gills on abdominal segment 6 is an example of an apomorphy that must be used with caution. It cannot be used to deduce common ancestry of lineages, because, based on parsimony, it evidently occurred convergently in *Nadinella*, *Lestagella* and *Teloganodes*. It does serve, however, as a defining autapomorphy for the *Teloganodes* lineage, and as such is critical to defining *Teloganodes* as a monophyletic genus distinct from its sister *Macafertiella* lineage.

There are certainly instances when the loss of gills on particular abdominal segments is of importance for deducing common ancestry. The loss of gills on abdominal segment 2, for example, is a synapomorphy that defines the entire family Ephemerellidae, and the loss of gills on abdominal segment 7 in Teloganodidae is a synapomorphy that helps define one of two major, most basal clades within the family [see apomorphy 11 (Fig. 1, Table 2)] that we consider a separate subfamily (see below).

It might be argued that the reduction of the median caudal filament is so widespread in disparate lineages in Ephemeroptera, and thus so highly subject to homoplasy, that it is of little or no use in deducing phylogeny. It is, moreover, highly probable that in certain lineages the median caudal filament becomes secondarily re-developed and lengthened from the reduced condition (see McCafferty 1979). Nonetheless, loss of the middle tail in certain individual monophyletic groups of mayflies recognized at the family level, such as among Teloganodidae or Heptageniidae larvae, is an obvious independent evolutionary event that provides cladistic information. The common ancestry of *Macafertiella* and *Teloganodes* was deduced in part by using the only instance of this loss in the Teloganodidae. Furthermore, this common ancestry is supported by two other synapomorphies [see apomorphies 26-28 (Fig. 1 and Table 2)]. On the other hand, if one were developing a cladogram of the entire family Baetidae, the innumerable instances of reduction of the middle tail would obviously constitute misleading information for deducing major lineages.

Dorsal abdominal tubercles are developed on the larval abdomens of many mayflies, but are probably most common among the Ephemerellidae and Teloganodidae. Such tubercles have certainly developed as independent apomorphies in such groups as the genus *Acanthiops* of the family Baetidae (see Waltz and McCafferty 1987, Barber-James and McCafferty 1997), and the genus *Anepeorus* of the family Heptageniidae (as *Spinadis* in Edmunds and Jensen 1974, Edmunds et al. 1976). As first suggested by Demoulin (1967), the general habitus of the larvae of certain *Acanthiops* are amazingly similar to some Teloganodidae, but this is especially true for the recently discovered *Macafertiella* because of its single row of tubercles and two-tailed condition. Such tubercles are even found independently developed in other aquatic insect orders, such as certain stoneflies (see e.g., Illies 1961, Hynes 1970).

With respect to the current study, we hypothesize that dorsal abdominal tubercles were present in the immediate common ancestor of the Teloganodidae and Ephemerellidae because of their relative pervasiveness in these groups. We also infer that ancestrally they occurred in two rows on the abdominal terga. This inference derives from the fact that the double row condition is found throughout the Ephemerellidae and in three lineages of Teloganodidae. Based on other data, the teloganodids lineages with double rows represent one of the two basally derived clades within the Teloganodidae (*Austremerella* + *Vietnamella*), and the somewhat plesiotypic *Nadinella* of the latter's sister group. In other Teloganodidae, the double tubercle rows have either become a single median row, or tubercles are secondarily lost. A glimpse of how this evolution has perhaps easily occurred is seen in the variation of tubercles found in individual larvae of *Nadinella* (Figs 5, 74-76), where on various terga, the tubercles of a pair can be broadened and juxtaposed medially, coalesced into a single broad

protuberance, and sometimes appear as a single median tubercle. In other teloganodids, there is either a single row of dorsal abdominal tubercles (*Ephemerellina*, *Lithogloea*, *Macafertiella*, and plesiotypic species of *Teloganodes*) or such tubercles have entirely disappeared (*Lestagella* and apotypic species of *Teloganodes*). Considering the cladogram, the single row condition appears to have preceded the loss of tubercles which has occurred independently in *Lestagella* and within *Teloganodes*.

A distinctive setal fringe is developed on the entire cephalic margin of the *Lestagella* + *Macafertiella* + *Teloganodes* clade. It is independently developed, but only laterally in *Vietnamella*. Other cases of homoplasy are found in other families of mayflies, e.g., *Haplohyphes* in the Leptohyphidae (see Lugo-Ortiz and McCafferty 1995), *Diceromyzon* in the Tricorythidae [present but not figured by Demoulin (1954a)], and *Epeorus* in the family Heptageniidae (see e.g., Edmunds et al. 1963).

Abdominal posterolateral processes are well developed in many different lineages of Ephemerellidae [to the extreme in *Timpanoga* (see McCafferty and Wang 1994)] and some other families of mayflies. They are also well developed independently in *Lithogloea*, somewhat in *Lestagella*, and in at least one species of *Teloganodes* within the Teloganodidae. In *Lithogloea*, the processes are sharply attenuated; in *Lestagella* and *Teloganodes*, they are not as attenuated.

Although it is somewhat difficult to determine the exact plesiomorphic state of the mandibular incisors among teloganodids by using outgroup methodology, a generalized form of the armature of the more variable left mandible appears to be represented by the mandibles of *Nadinella* (Fig. 32) and most species of *Teloganodes* (Fig. 36), for which almost exact matches can be found among the Ephemerellidae (see e.g., Fig. 40 of Allen and Edmunds (1963b)). In these mandibles, the incisors are separate, only slightly divergent from each other, oriented distally, and the outer incisor has three blunt denticles. Only slight modifications of this plan are found in *Ephemerellina*, *Lithogloea*, and *Macafertiella*. However, in *Lestagella* (Figs 25, 34), the incisors are completely reduced; in *Vietnamella* (Figs 21, 30), the incisors are fused and laterally oriented; and in at least one species of *Teloganodes* (Figs 28, 37), the outer incisor is blunt and without denticles and the inner incisor is highly reduced. Differences in the incisors were of no use cladistically, possibly owing to the adaptive nature of such structures. Caution must always be used in assessing the condition of the incisors of mayfly mandibles, even for diagnostic use, because they can become worn in long-lived instars. There is also evidently some change in characteristics from young to older instar larvae, for example, see comparative mouthpart figures of *Lestagella* provided by Demoulin (1970, Fig. 15).

Other characteristics of the mandibles did provide valuable cladistic information, including the phenoclinical development of the long mediolateral seta as discussed above. In addition, there has been a strong tendency for the body of the mandible to become narrowed in teloganodids [see apomorphy 15 (Fig. 1) (Table 2)]. This may be phenoclinical, but we cannot be sure. In the clade having the narrowed mandible, *Nadinella* is most apotypic and also has a mandible that does not appear as narrowed as others in the clade. Outside of this clade, *Vietnamella* also shows some narrowing of the mandibles, and while this may be viewed as generally convergent, it is different from that seen in the others because the mandibles are abruptly narrowed in the basal two-thirds, with the apices remaining broad. A small patch of setae occurs on the medial margin near the apices of the mandibles of Ephemerellidae and Teloganodidae; however, it is lost in the left mandible of the clade made up of *Nadinella*, *Lithogloea*, *Lestagella*, *Macafertiella*, and *Teloganodes*. The only incongruent character state distribution is that it occurs weakly developed in *Macafertiella*. Since so many other synapomorphies (Fig. 1) corroborate the phylogenetic placement of *Macafertiella*, we can only assume that the setal patch was re-developed subsequently in *Macafertiella*.

Other characters of the mouthparts were of some value, but quite predictably were always subject to some degree of homoplasy. Dorsal setal patterns on the labrum evolved from generally scattered dorsal setae, similar to that found in *Austremerella* and *Ephemerellina*, which happen to be the most plesiotypic lineages in both of the major clades. Setae become restricted to irregular, transverse rows in the midregion of the labrum [see apomorphy 14 (Fig. 1, Table 2)]. The most ordered setal row is found in *Macafertiella* amongst those with this condition. In *Vietnamella*, the generally scattered setae have independently become absent from the basal half of the labrum, but remain relatively scattered throughout the distal half.

As mentioned above the phenoclinical development of fusion in the glossae of the labium is instructive, but in addition to this, the apical shape of the paraglossae is important. The plesiomorphic condition is one in which the paraglossae are bluntly pointed apically, and sometimes this point is oriented medioapically. In the clade of *Lestagella* + *Macafertiella* + *Teloganodes*, the apices of the paraglossae have become narrowly rounded. A different apomorphy of this bi-directional character is seen in *Vietnamella*, in which the apices of the paraglossae have become flat and truncate [see apomorphies 6 and 23 (Fig. 1, Table 2)].

Maxillary palpi are absent in all but *Vietnamella* among the Teloganodidae, perhaps indicating that the palpi were lost independently in *Austremerella* and the common ancestor of the other major clade (Fig. 1). An alternative explanation for this would be that the palpi were absent in the common ancestor of the family Teloganodidae, but re-appeared in the aberrant *Vietnamella* lineage. Generally, structures are not expected to reappear (Ross 1974) but there are exceptions. Small nodule-like rudiments of the maxillary palpi are present on the maxillae of many *Teloganodes*.

Finally, with respect to wing venation in the Teloganodidae, the appearance of a free, additional longitudinal vein in the stigmatic area of the forewing, with numerous small cells, or cellules, on either side of it (Figs 80-82) is an important synapomorphy for the *Austremerella* + *Vietnamella* lineage [see apomorphy 2 (Fig. 1, Table 2)]. Somewhat similar modifications of the forewing have evolved independently in some other mayflies. For example, in certain Heptageniidae genera, the stigmatic area contains a secondary longitudinal vein, but cellules are not as developed, and in certain genera of a number of families, stigmatic crossveins may be more or less anastomosed, sometimes giving the impression of cellules (see Edmunds et al. 1976). Within the Teloganodidae, in fact, the forewings of African genera of Teloganodinae show some slight reticulation or tendency for such in the stigmatic area (Figs 83-86). Although this cannot be confused with the *Austremerella* + *Vietnamella* synapomorphy, it does indicate that the common ancestor of the Teloganodidae probably had some slight reticulation in the stigmatic area. The shortening of IMP compared to MP₂, and its detachment from MP₂ in the forewings is a stable and important apomorphy for establishing *Lithogloea* in the *Lithogloea* + *Lestagella* + *Macafertiella* + *Teloganodes* clade [see apomorphy 18 (Fig. 1, Table 2)].

PHYLOGENETIC CLASSIFICATION

Although cladistic methods have recently been employed to hypothesize phylogeny in Ephemeroptera (e.g., McCafferty 1979, McCafferty and Edmunds 1979, Peters 1980, Savage and Peters 1983, Domínguez 1995), it is only more recently that phylogenetic classifications have been strictly derived from cladistic data, or cladograms (Bae and McCafferty 1991; McCafferty 1991a, 1991b; McCafferty and Wang 1994; Lugo-Ortiz and McCafferty 1996; Barber-James and McCafferty 1997). Based on our cladistic analysis of the Teloganodidae, we also present a strictly phylogenetic classification as elaborated and endorsed in general by Wiley (1981) and in particular with respect

to Ephemeroptera by McCafferty (1991a). We also incorporate sequencing conventions (Nelson 1972, 1973), which were thoroughly discussed by McCafferty and Wang (1994) with respect to their application to the *Timpanoga* complex (Ephemerellidae).

The strictly phylogenetic hierarchical classification of the Teloganodidae is given in Table I. As such, the cladogram (Fig. 1) is entirely reproducible from the linear classification. The most basal bifurcate branching in the cladogram (Fig. 1) is reflected in the classification as the subfamilial delineation.

Within the subfamily Teloganodinae (Fig. 1), sequential branches of species group OTUs are recognized as separate genera by sequencing. All such genera are further defined by autapomorphies. This is both a phylogenetic and practical classification because all the genera as such are easily distinguishable in both the larval and adult stages (see the Key to Genera, above). It would be tempting to recognize some highly specialized species in *Teloganodes* as a separate taxon, either genus or subgenus; however, the remainder of *Teloganodes* would be left without an autapomorphy to define them, and thus would essentially become a non-allowable paraphyletic group.

BIOGEOGRAPHY

The Teloganodidae can be viewed as a group of Old World Gondwanan origin based on its restricted distribution in the Orient, Australia and southern Africa. Its sister family Ephemerellidae is essentially Holarctic and Laurasian. Edmunds (1972, 1975, 1981, 1982), Bae and McCafferty (1991), and McCafferty et al. (1992) have argued that mayflies are ideal candidates for studying historical biogeography because of the order's antiquity, restriction to freshwater as larvae, short-lived and fragile nature of alate stages, and conservative vagility. Such qualities may be expected to be particularly amenable to reflecting ancient patterns affected primarily by vicariance (Croizat et al. 1974), as could be expected by Southern Hemisphere lineages old enough to have participated in continental drift. By superimposing the distributions of the genera of Teloganodidae (Table 1) on the cladogram of the genera (Fig. 1), it is possible to hypothesize certain aspects of the historical biogeography of the various lineages (Ross 1974, Rosen 1975).

We hypothesize a Gondwanan origin for the Teloganodidae prior to the initial breakup of Gondwanaland. The family's restriction to the Old World Southern Hemisphere and tropical Asia would suggest this. We hypothesize that the subfamily Austremerellinae originated prior to the breakup of Gondwanaland, subsequently becoming isolated in Australia and more recently dispersing through Wallacea to the tropical Orient [most probably circa 25 to 17 mya (million years ago) (Raven and Axelrod 1974, Hamilton 1979)], where it is now represented by the relatively aberrant genus *Vietnamella*. The subfamily is represented in Australia by the phylogenetic relict *Austremerella*, with an ancestry that possibly dates to the Triassic. While dispersal from Australia to the Orient has been relatively uncommon and relatively recent (Raven and Axelrod 1972, Hamilton 1979), models of earth history [with Australia and the Orient at somewhat opposite ends of Pangaea (see e.g., Pielou 1979)], preclude other explanations at this time.

We hypothesize that the subfamily Teloganodinae arose in Gondwanaland and subsequently became isolated in temperate South Africa. A considerable biota in temperate South Africa is regarded as Gondwanan in origin and has been referred to as the palaeogenic [not to be confused with the Paleogene period of Tertiary (see e.g., Stanley 1989)], or old, element in the Afrotropics (e.g., Brinck 1955a, 1955b; Stuckenberg 1962; Harrison 1965). *Ephemerellina*, *Nadinella*, and *Lithogloea* are restricted to the mountainous southern temperate area of the Western Cape Province of South Africa. *Lestagella* apparently has a somewhat more extensive range that includes mountainous areas of

extreme southeastern Africa as well. We have been able to substantiate Eastern Cape records of *Lestagella*. Reports of *Lithogloea* outside of the Western Cape, however, are apparently erroneous (see especially Distribution under *Lithogloea* and *Lestagella* in the Account of Taxa, above). In any case, all African genera qualify as temperate Gondwanaland, phylogenetic relicts, the origin of which can be traced to 135 to 200 mya (see, e.g., Pielou 1979) and possibly much earlier.

Harrison (1965) considered the leptophlebiid mayfly genera *Aprionyx* Barnard and *Castanophlebia* Barnard as South African representatives of an "old-element, palaeo-endemic" fauna because they were thought to have affinities with South American and Australasian Leptophlebiidae. Peters and Edmunds (1964) suggested that the South African leptophlebiid genera *Aprionyx* and *Adenophlebia* Eaton had Paleontarctic affinities. Harrison (1965) included *Ephemerellina* and *Lithogloea* (the only South African genera of Teloganodidae recognized at that time) as only candidates for inclusion in his "old-element" category because their broader biogeographic affinities were not known outside of South Africa. Our phylogenetic data on the Teloganodidae substantiate the inclusion of African teloganodids in his biogeographic grouping.

The African genus *Lestagella* and two, more apotypic, Oriental genera *Macafertiella* and *Teloganodes* make up the most derived clade in the subfamily Teloganodinae. We hypothesize that the origin of this clade was temperate South Africa, and that it originated relatively early. Whereas all other genera of African Teloganodidae are evidently restricted to the Western Cape, we have examined specimens of *Lestagella* from the Eastern Cape and also believe that other specimens from the Amatola Mountains, Eastern Cape, tentatively identified as *Lithogloea harrisoni* by Crass (1947) are either *Lestagella* or *Ephemerethus* (Tricorythidae). Harrison and Agnew (1962) noted that teloganodids had been seen from the Transvaal and as far north as Malawi, but those reports are attributable to *Ephemerethus* based on our examination of material (see Distribution under *Lithogloea* and *Lestagella*, in the Accounts of Taxa, above). *Lestagella*, therefore, appears to be both part of the temperate Gondwanaland element but also may be typical of many such groups in Africa in having become distributed eastward and sometimes northward along mountain chains (Harrison 1965). The geography of *Lestagella* would appear to be compatible with the transitional nature of this lineage depicted by its phylogenetic position (Fig. 1) and its hypothesized more recent participation as a faunistic link between the African and Oriental members of the subfamily Teloganodinae [the trans-Indian Ocean track (Craw 1988) as seen in the Teloganodidae].

The *Macafertiella* + *Teloganodes* lineage became isolated and radiated in tropical Asia. Given our hypothesis of a temperate southern Africa origin for the Teloganodinae, the trans-Indian Ocean track of this group could be explained by movement of the Indian subcontinent northward from southern Africa-Madagascar landmass [beginning circa 150 mya and culminating circa 45 mya (e.g., see Kummel 1970)]. Dispersal during pluvial periods through Asia Minor [perhaps circa 17 mya (Raven and Axelrod 1974)], as for example has been hypothesized for certain mayfly genera such as *Afromera* (McCafferty and Gillies 1979) and *Povilla* (Hubbard 1984), does not appear to be a viable possibility. This is because teloganodids are entirely absent from Asia Minor and east Africa, where they would be expected if there had been such a dispersal. There are examples of a strong Afro-Oriental affinity in many other lineages of mayflies, sometimes with genera distributed exclusively in southern Africa and the Orient (e.g., see Gillies 1957, Peters et al. 1964, McCafferty and Edmunds 1973, Edmunds 1979, Waltz and McCafferty 1994, Provonsa and McCafferty 1995). The Afro-Oriental relationship may be special among the teloganodids and some Leptophlebiidae because of their general restriction to mountain streams. Today, the Oriental teloganodid fauna apparently consists of two independently derived lineages of Teloganodidae, represented by the subfamilies Austremerebellinae and Teloganodinae.

Based on all of the above, one might expect Teloganodidae (esp. Teloganodinae) to be a reasonable candidate for distribution in Madagascar. However, as pointed out by Edmunds (pers. comm.), one should not always expect a uniform biota in all the divided parts of a former landmass, as for example is the case with *Tricorythus* Eaton (Tricorythidae), because few genera and species are widespread on the present landmasses. In the case of the Teloganodidae, Madagascar is evidently not represented in the trans-Indian Ocean track. On the other hand, in the case of the *Teloganella* complex of genera (*Manohyphella*, *Provonshaka* McCafferty and Wang, and *Teloganella*), which are currently regarded in the Tricorythidae (McCafferty and Wang 1995, Wang et al. 1995), it is Africa that is excluded from representation in their trans-Indian Ocean track.

Consideration of the relict genera of Teloganodidae in South Africa and Australia indicates that they are typical of other known phylogenetic, or evolutionary, relicts among the Ephemeroptera in several respects. Interesting comparisons can be made with the Amphinotic families such as Ameletopsidae, Oniscigastriidae, Nesameletidae-Rallidentidae, and Coloburiscidae that consist only of genera that are phylogenetic relicts of Transantarctica and are now found only in Australia, New Zealand, and southern temperate South America (see Edmunds 1975, McCafferty 1991a). The genera are small, with only one or very few species each, and they are highly distinctive but at the same time demonstrate some degree of convergence among relatives. These common characteristics of such taxa are predictable by their age and the decimation of related species (after Gould 1989). Such phylogenetic relicts should probably be referred to as "survivors" rather than relicts, as has been aptly pointed out by Udvardy (1969). Such archaic forms figuratively have outlived all other members of once possibly thriving taxa, and on a grand scale, they fit the final stage of the taxon cycle elaborated by Ricklefs and Cox (1972), in that descendant species have dwindled, leaving only a few perhaps fortuitous survivors.

None of the Transantarctic, Amphinotic families of mayflies mentioned above are found in Africa (or Madagascar or the Indian subcontinent). On the other hand, no Teloganodidae show the Transantarctic pattern. In generally accepted models of the breakup of Gondwanaland (e.g., Wegener 1929, Kummel 1970, Colbert 1973), Africa separated from Transantarctica prior to the breakup of Transantarctica, respectively into West and East Gondwana. From this, one can conclude that the teloganodid lineages represented in South Africa and Australia can be traced to southern Pangaea, at least to 200 mya. This makes them as old or older than the strictly Amphinotic groups, which may have originated subsequently in West Gondwana, showing the classical patterns that are apparent in some more well known organisms, for example the flightless birds (see Cracraft 1973). This being the case, some adjustment may be required among ephemeropterists with respect to any "conventional wisdom" that extant pisciform mayflies are the oldest living mayflies.

Unfortunately, scant Ephemeroptera fossil data are available from the Southern Hemisphere to shed additional light on these theories (see McCafferty 1990). Triassic mayfly fossils known from South Africa are not clearly related to any extant mayflies (Riek 1976, Hubbard and Riek 1977), and fossils from Australia are no older than the Lower Cretaceous (Jell and Duncan 1986). McCafferty (1997), however, has recently found an African fossil from Lower Cretaceous Lebanese amber that belongs to a clade of Atalophlebiine Leptophlebiidae containing both Amphinotic and Afrotropical extant genera. That paleontological data undoubtedly substantiates the primitive position of the clade hypothesized from phylogeny by Peters and Edmunds (1970). The only ancient fossil that has been assigned to anything possibly remotely related to the Teloganodidae was a partial larva of *Turfanerella tingi* (Ping), from the Jurassic in China, which was placed in the Ephemerellidae by Demoulin (1954b). Edmunds (1972), however, noted that this fossil was probably a pisciform mayfly. Despite the dearth of paleontological information available, cladistics of the phylogenetic relicts of Ephemeroptera have provided rather compelling data for inferring historical biogeography of the Teloganodidae.

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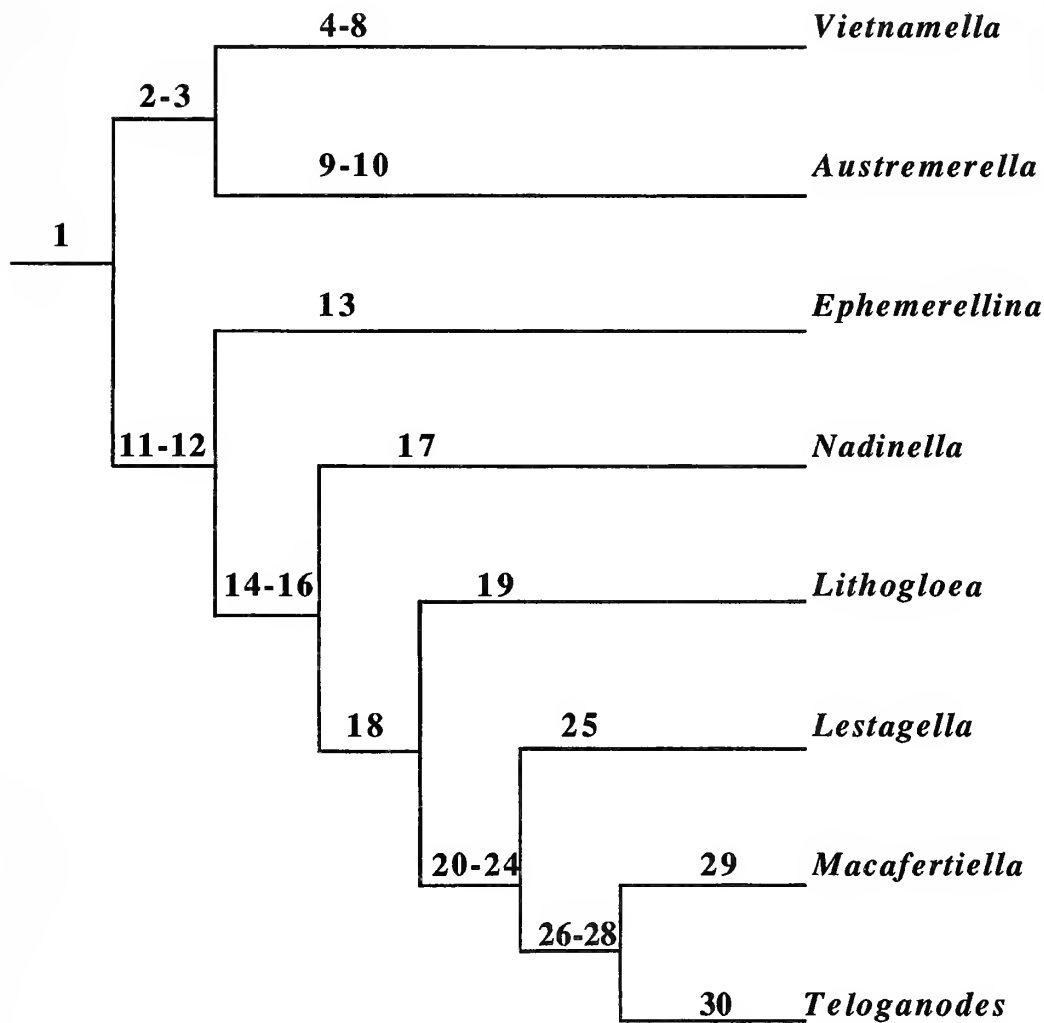


Fig. 1. Cladogram of monophyletic species groups of Teloganodidae.

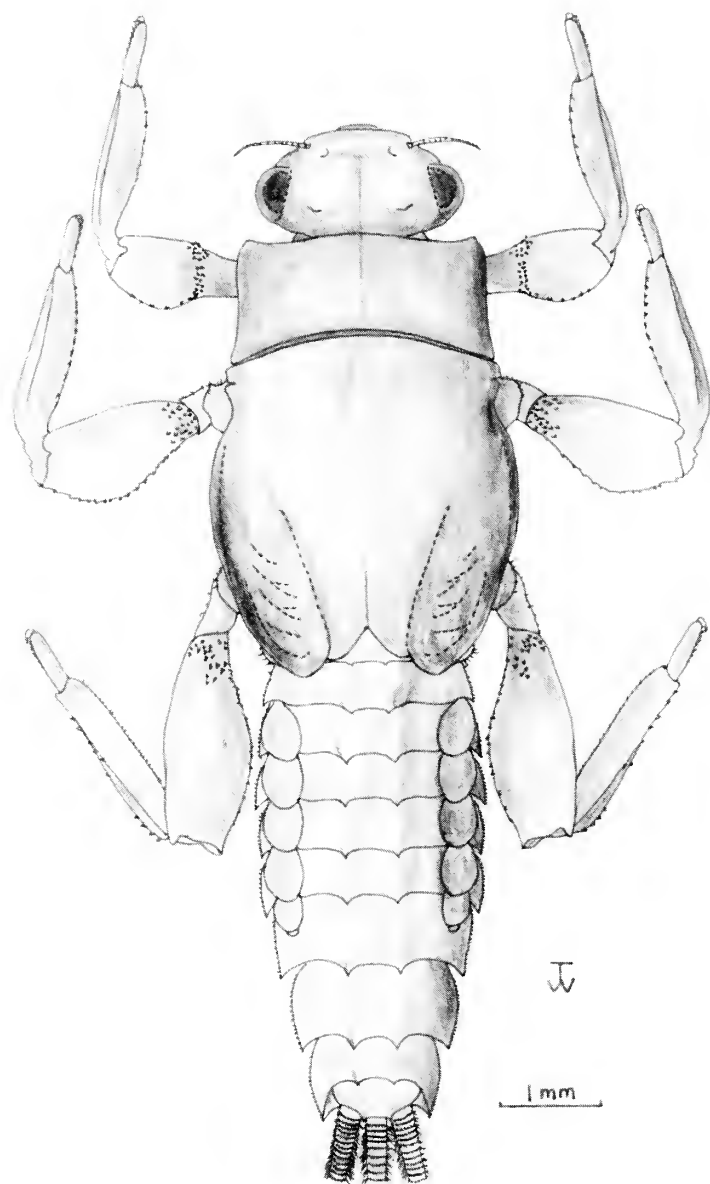


Fig. 2. *Austremerella picta*, larval habitus.

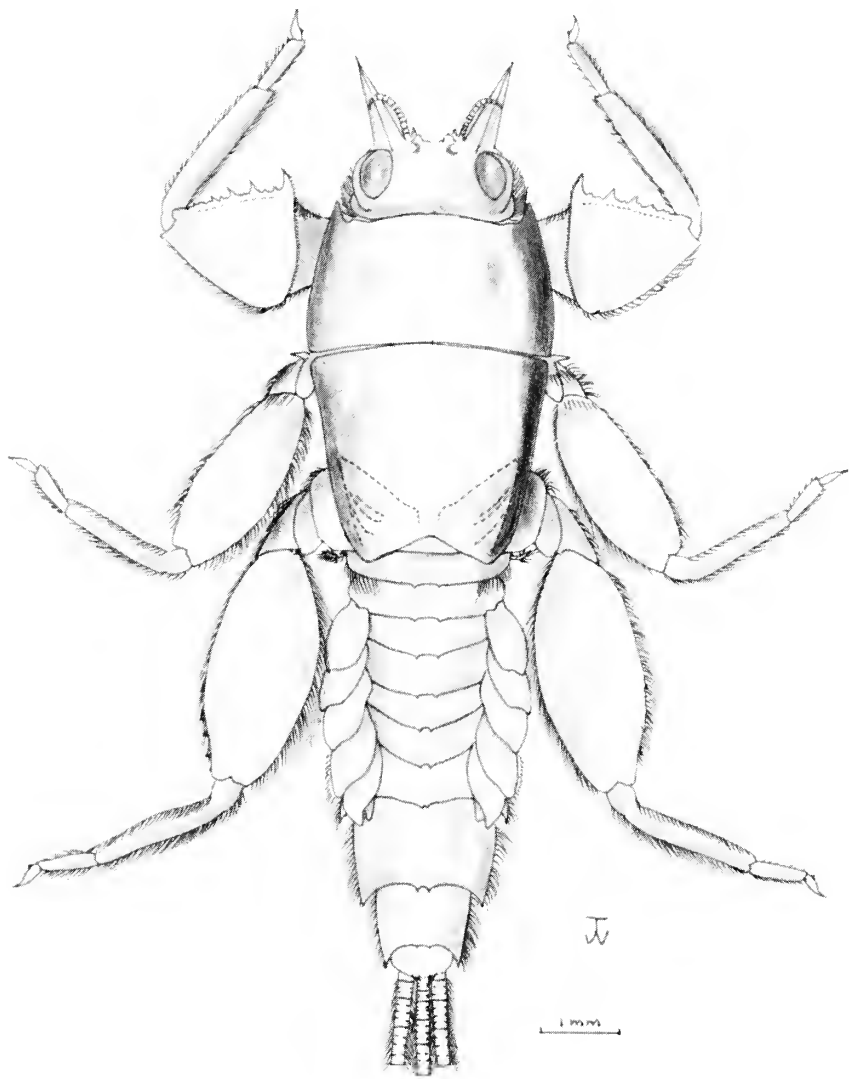


Fig. 3. *Vietnamella thani*, larval habitus.

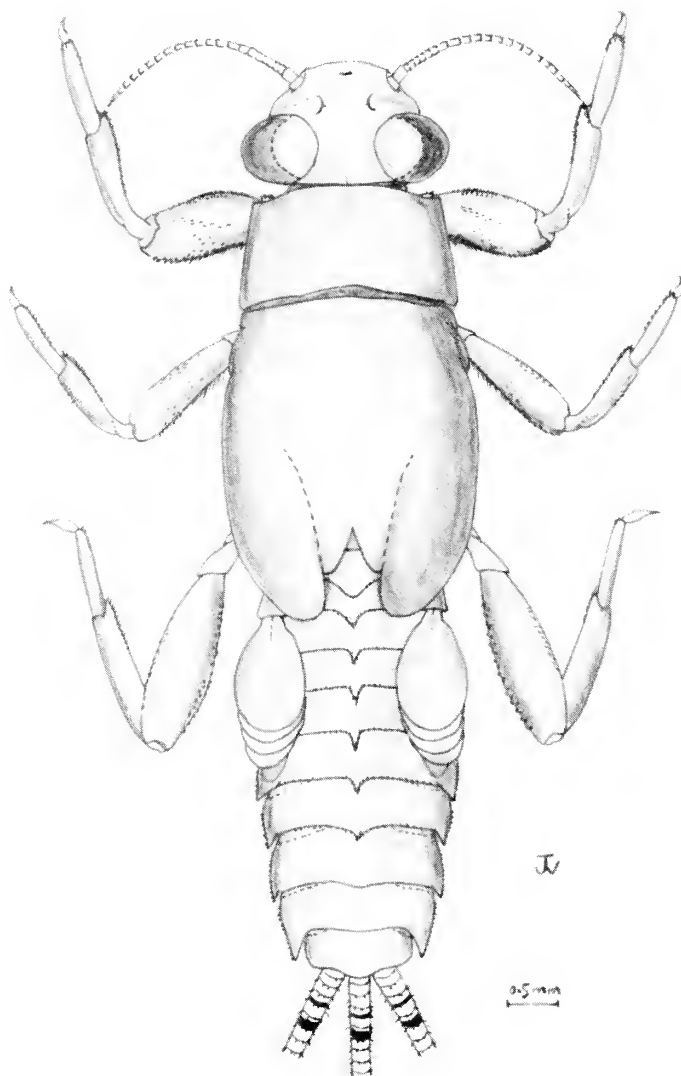


Fig. 4. *Ephemerellina barnardi*, larval habitus.

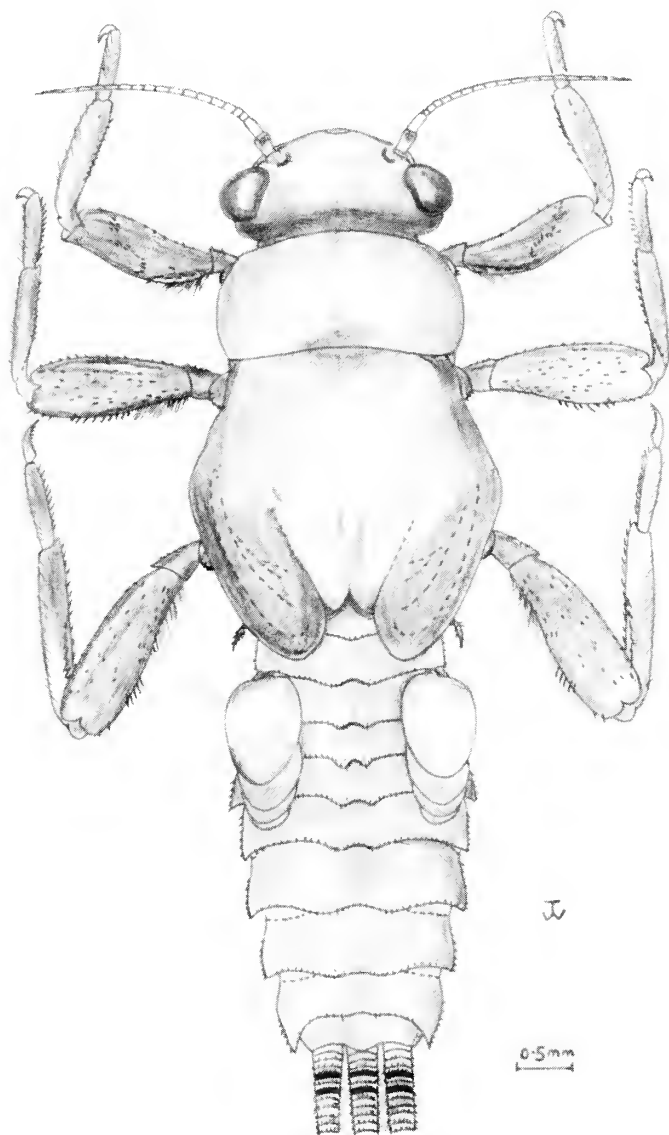


Fig. 5. *Nadinella crassi*, larval habitus.

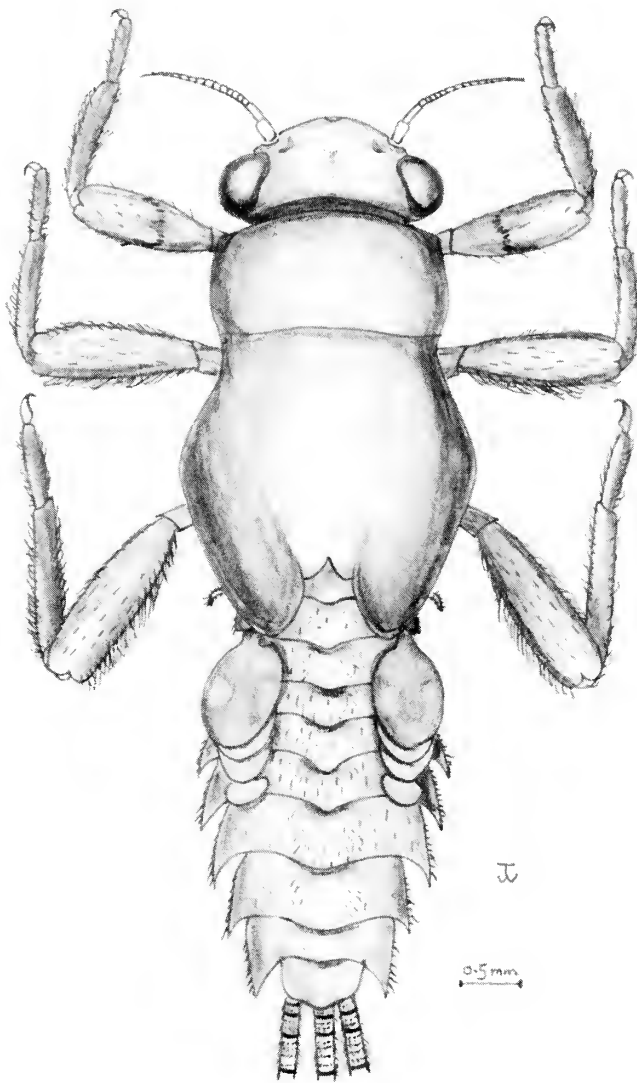


Fig. 6. *Lithogloea harrisoni*, larval habitus.

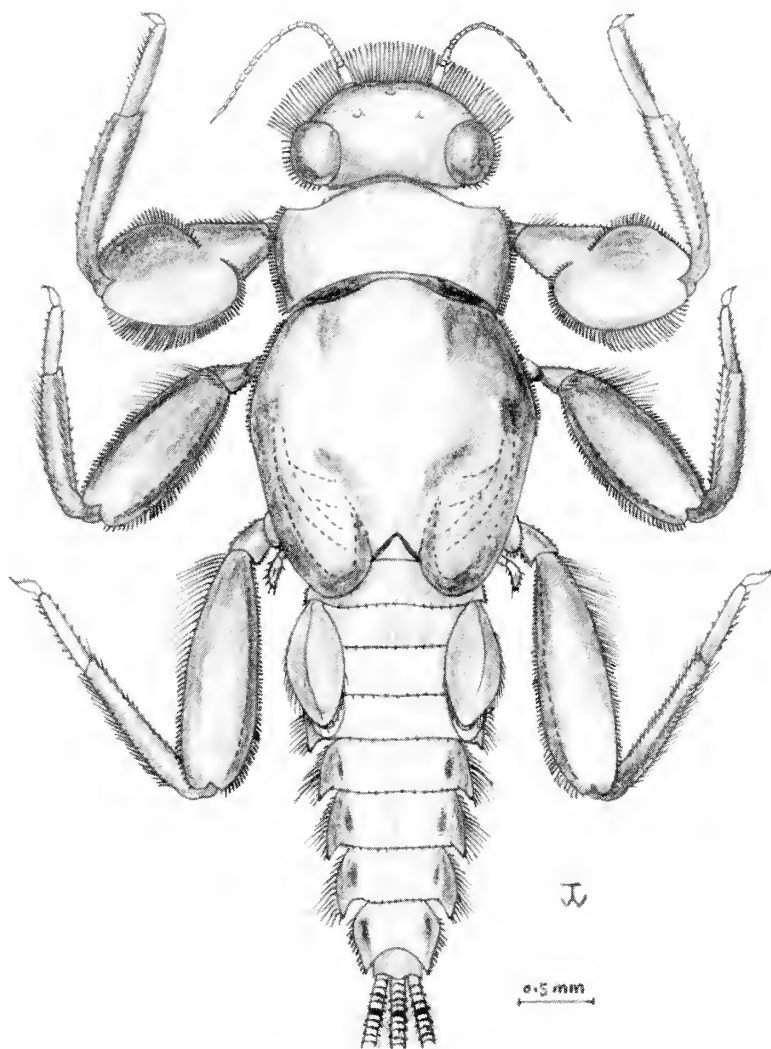


Fig. 7. *Lestagella penicillata*, larval habitus.

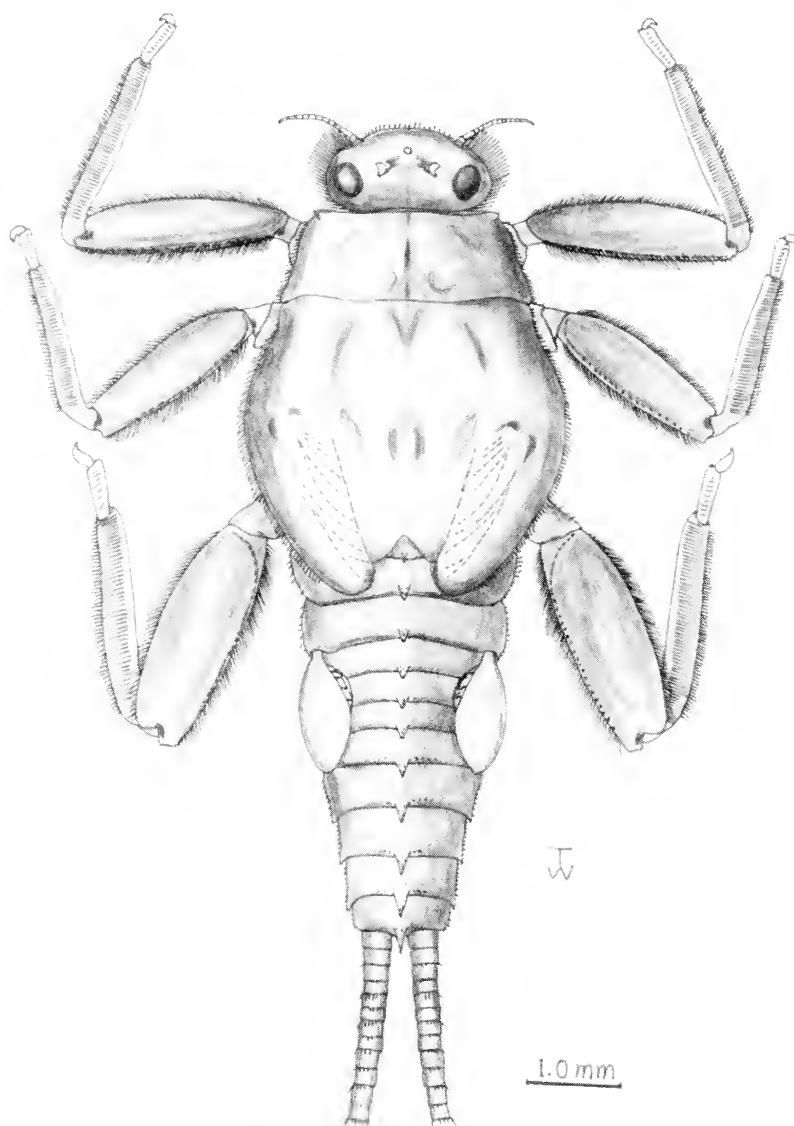


Fig.8. *Macafertiella insignis*, larval habitus.

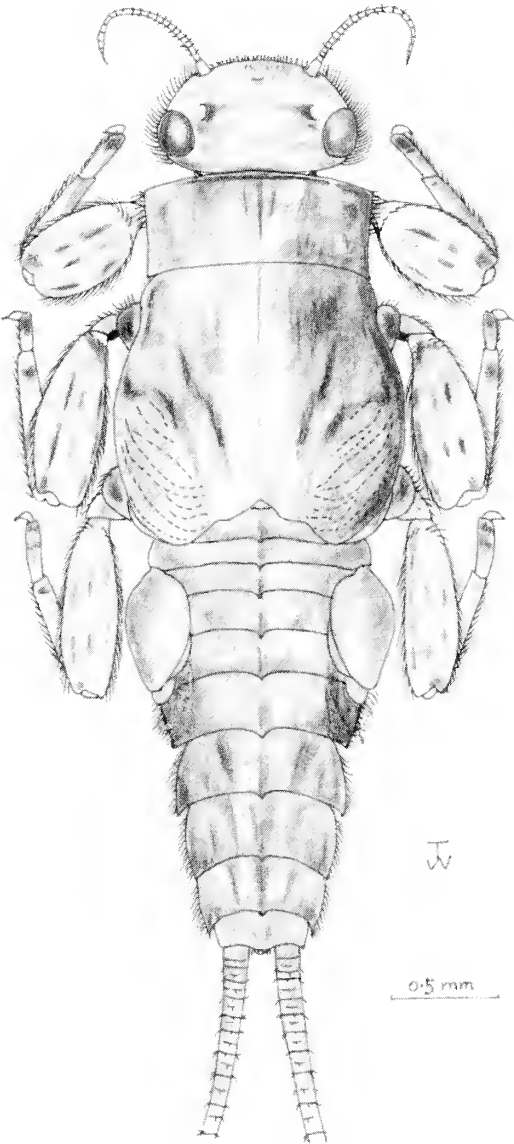


Fig. 9. *Teloganodes tristis*, larval habitus.

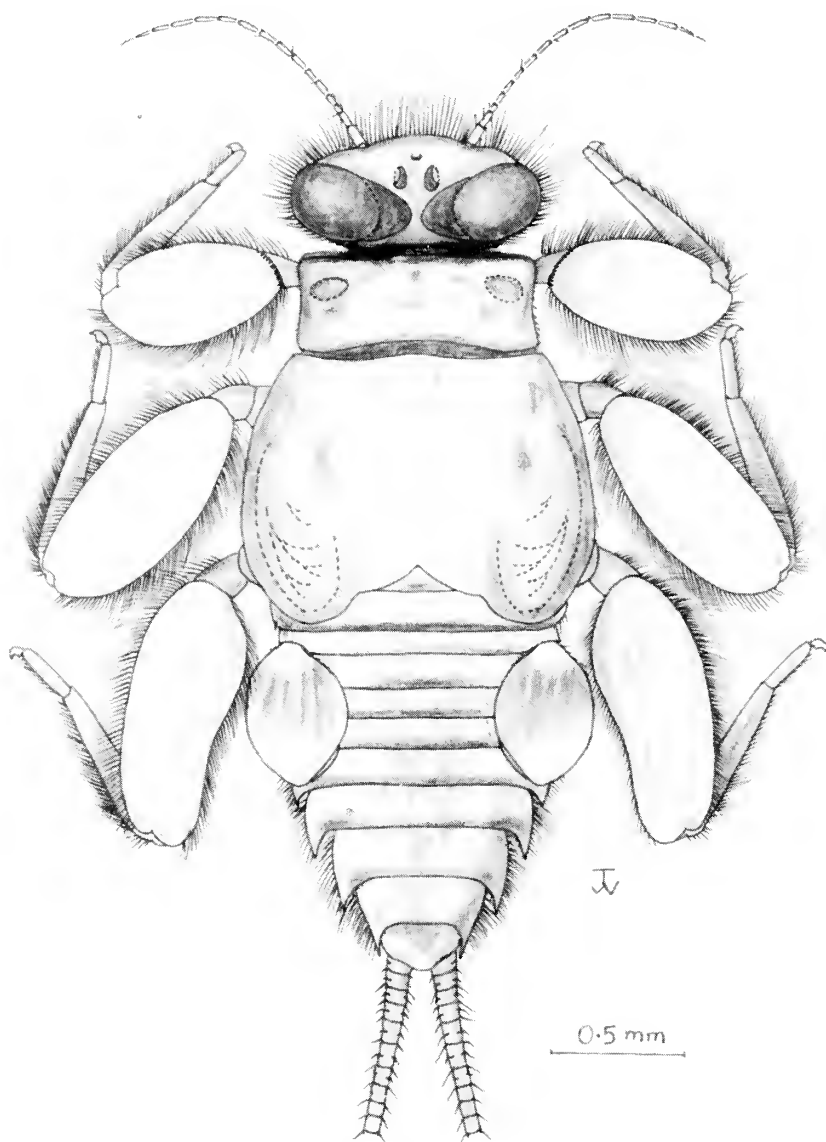
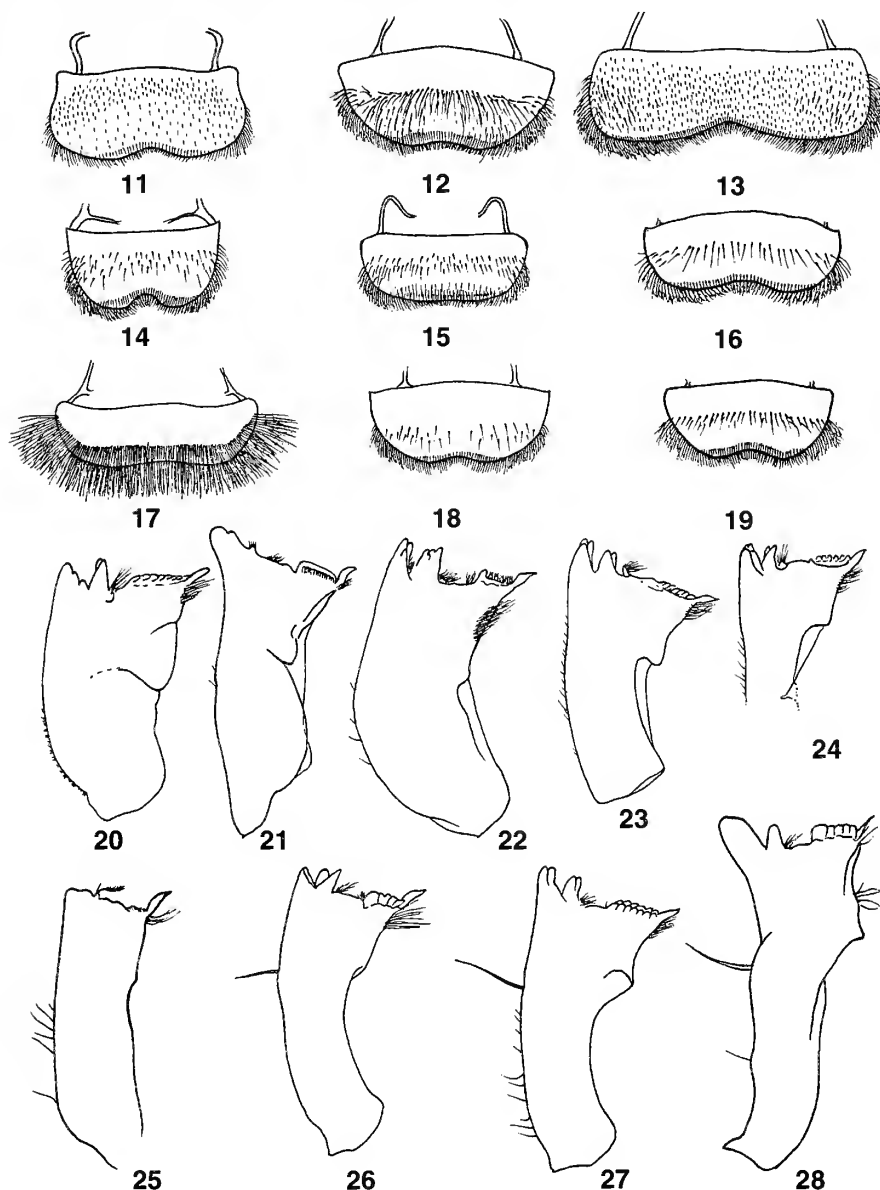
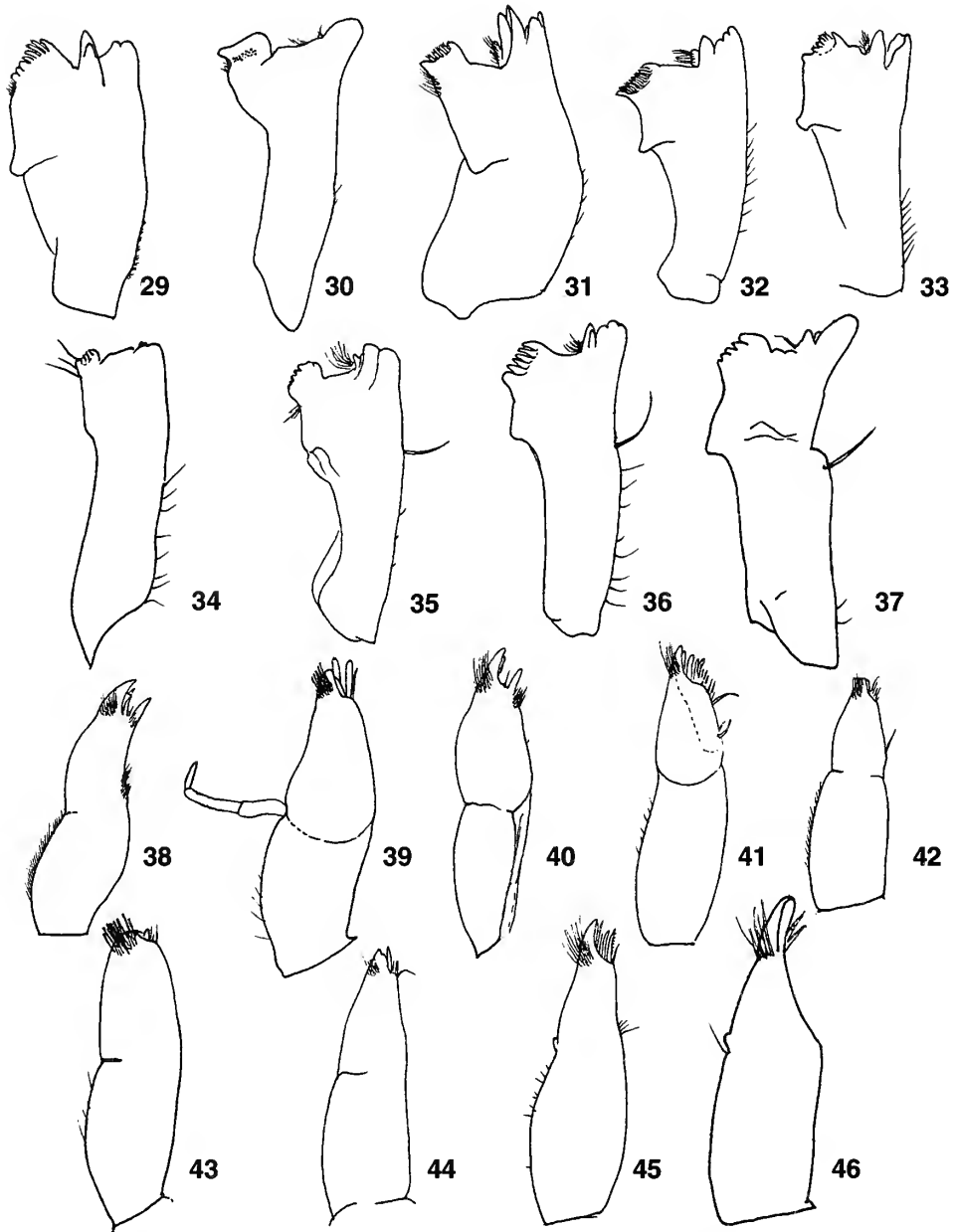


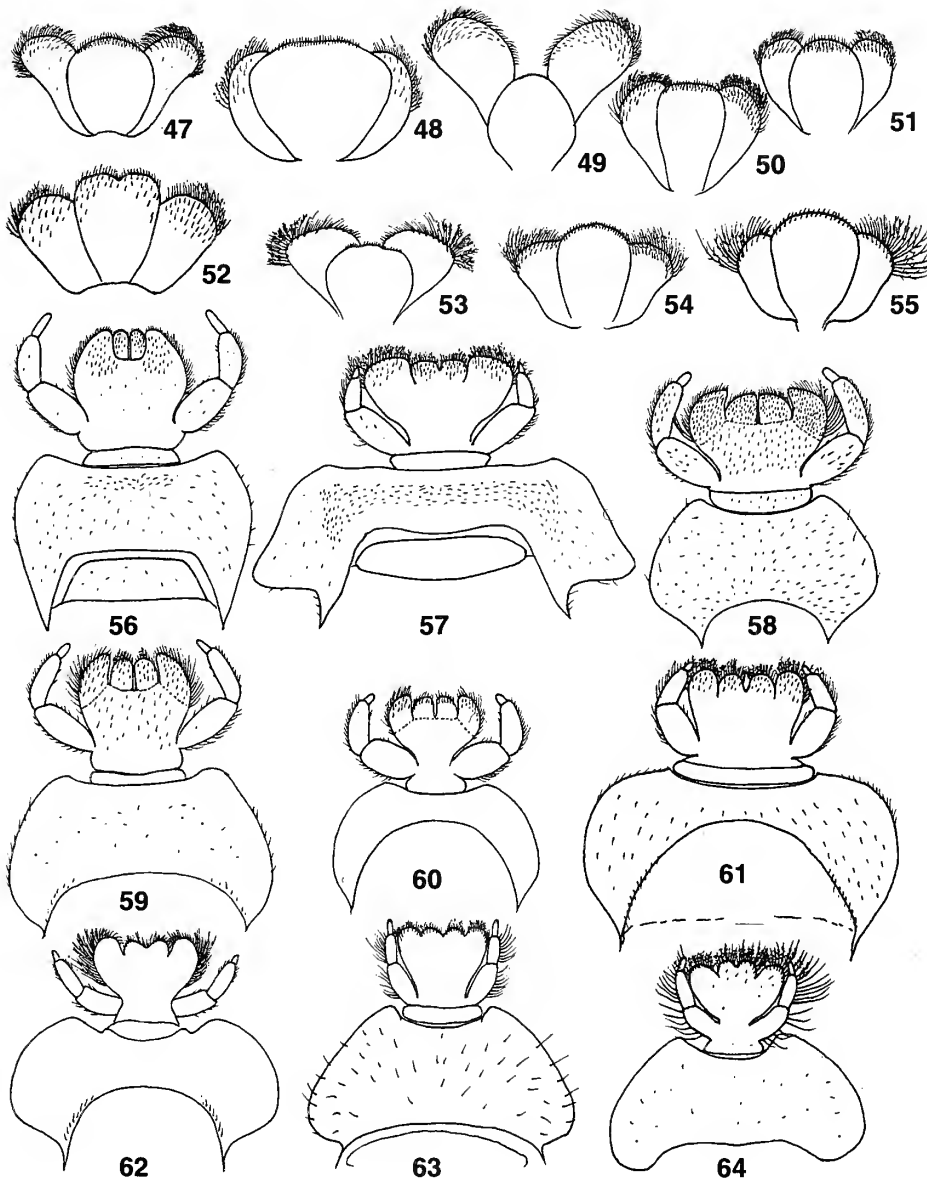
Fig. 10. *Teloganodes* sp., larval habitus.



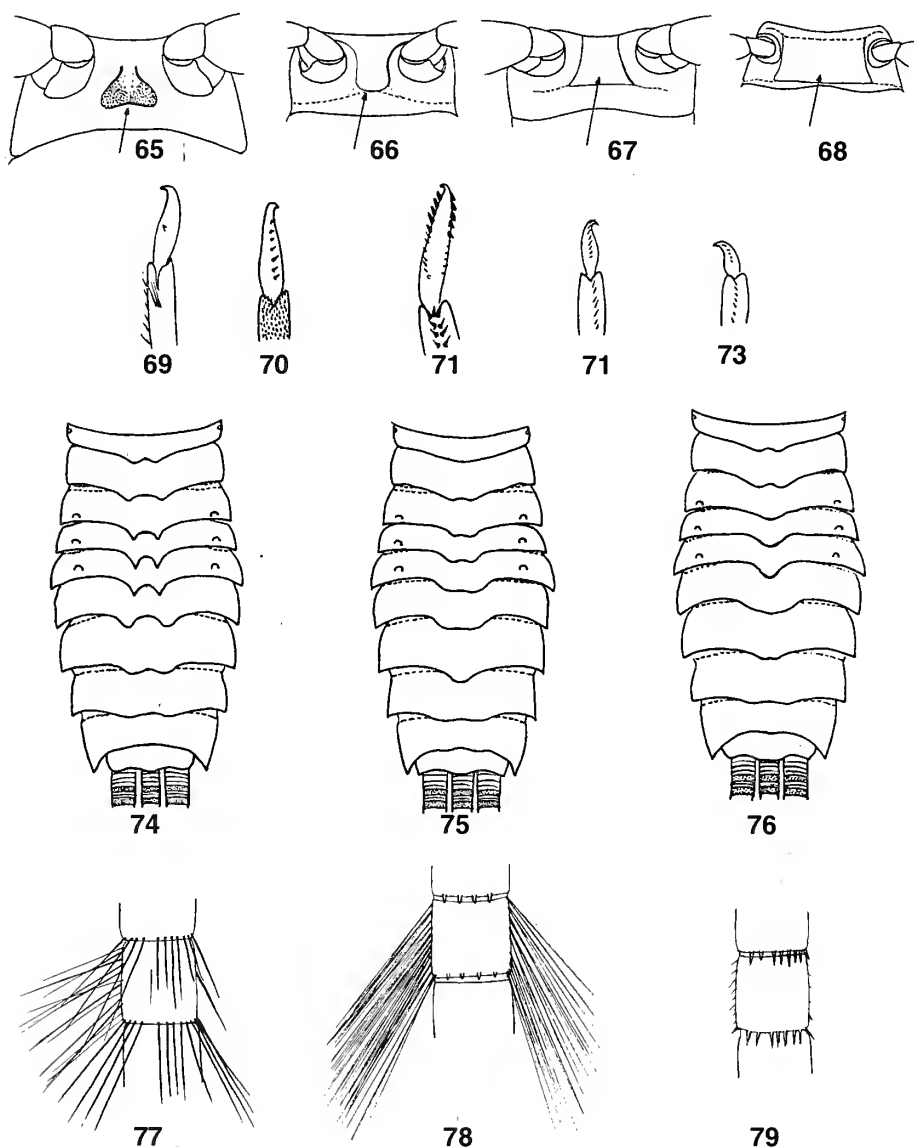
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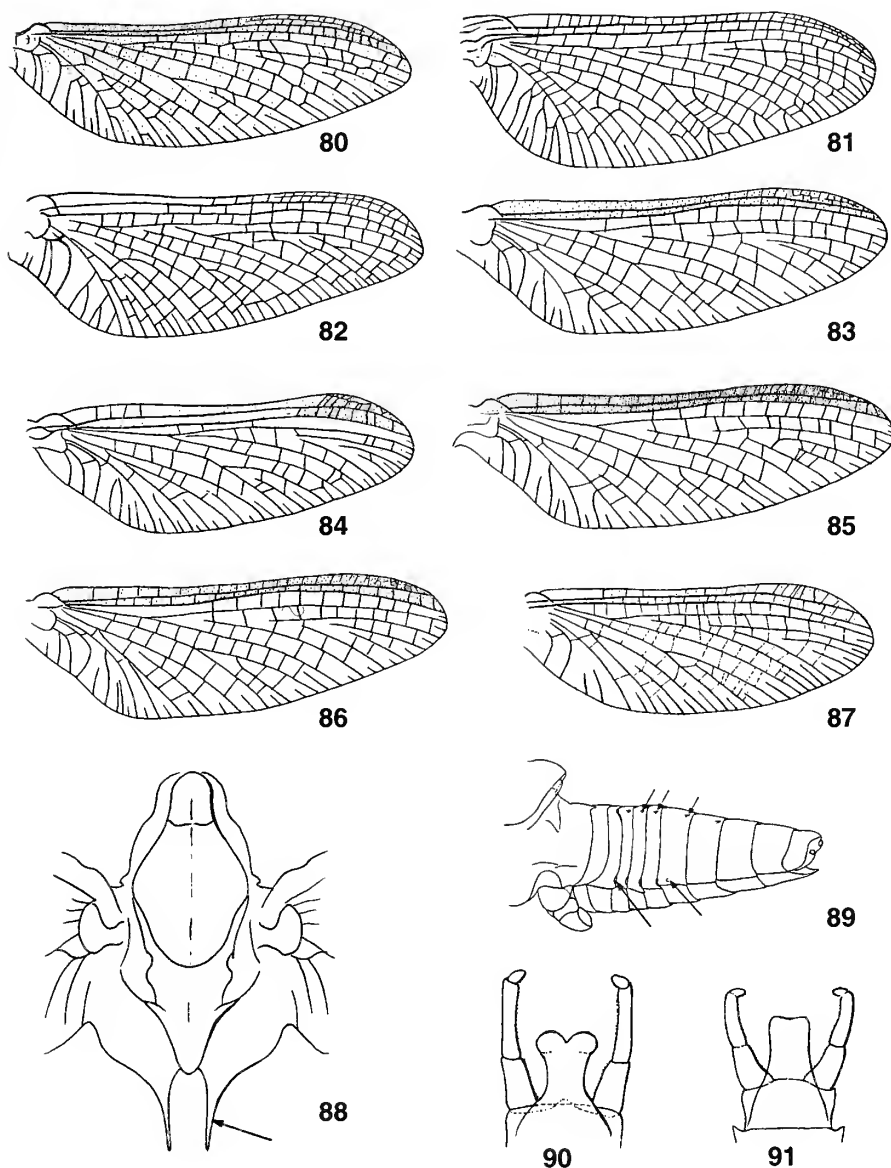
Figs 29-46. Left mandible and right maxilla. 29-37. Left mandible. 29. *Austremerella picta*. 30. *Vietnamella thani*. 31. *Ephemerellina barnardi*. 32. *Nadinella crassi*. 33. *Lithogloea harrisoni*. 34. *Lestagella penicillata*. 35. *Macafertiella insignis*. 36. *Teloganodes tristis*. 37. *Teloganodes* sp. 38-46. Right maxilla. 38. *A. picta*. 39. *V. thani*. 40. *E. barnardi*. 41. *N. crassi*. 42. *L. harrisoni*. 43. *L. penicillata*. 44. *M. insignis*. 45. *T. tristis*. 46. *T. sp.*



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